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Effect of weed water stress on postemergence herbicide activity

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Effect of weed water stress on postemergence herbicide activity

by

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PREFACE

Three passions, simple but overwhelmingly strong, have governed my life: The longing for love, the search for knowledge, and unbearable pity for the suffering of mankind....

With equal passion I have sought knowledge. I have wished to understand the hearts of men. I have wished to know why the stars shine. And I tried to apprehend the Pythagorean power by which number holds sway above the flux. A little of this, but not much, I have achieved.

Love and knowledge, so far as they were possible, led upward toward the heavens. But always pity brought me back to earth....

Bertrand Russell

One may know the world without going out of doors.
One may see the Way of Heaven without looking
through the windows.
The further one goes, the less one knows.
Therefore the sage knows without going about,
Understand without seeing,
If we know the general principle of things, we can know through thinking even if we do not travel. If we know the basis of things, even if we do not see them, we can understand the principle of right and wrong,
And accomplish without any action.

Lao Tzu

I who am now singing
Shall tomorrow be the mysterious, the dead,
The dweller of a magical and deserted
Sphere with no before nor after nor when.
So asserts mysticism. I believe myself
Unworthy of hell or of glory,
But I foretell nothing. Our story
Changes as do the forms of Proteus.
What errant labyrinth, what whiteness
Blind of splendor shall be my fate
When the end of this adventure turns over to me
The curious experience of dying?
I want to drink of its crystalline oblivion,
To be forever; yet not have been.

Jorge Luis Borges

The written word never captures all that has been attempted, but only the little that has been achieved.

Antonio Machado

INTRODUCTION

Shattercane (Sorghum bicolor [L.] Moench) and woolly cupgrass (Eriochloa villosa [Thunb.] Kunth) are important and expanding weeds in Iowa. These grasses demonstrate remarkable weedy characteristics such as a high growth rate, high reproductive capacity, secondary seed dormancy, and are difficult to control with conventional methods in grass crops.

New sulfonylurea herbicides present promising features for the control of these weeds with postemergence application to corn. The new products are highly selective, have exceptional herbicide activity, are used at very low rates, and exhibit very low toxicity to humans and animals. These characteristics are environmentally attractive and represent a low potential for environmental pollution from these herbicides.

Crops and weeds growing under water stress conditions suffer morphological and physiological changes that may affect the activity of postemergence herbicides. The

causes of poor herbicidal control of weeds growing under water stress are not clearly understood and have not been specifically studied for these herbicides.

The objectives of this research were to study physiological changes in shattercane and woolly cupgrass under different levels of water stress and to determine the effect of differential water status on the activity, retention, uptake, and translocation of postemergence sulfonylurea herbicides.

The research was divided in two parts: initial physiological studies of the effect of water stress on shattercane and woolly cupgrass, followed by studies of herbicide activity when applied to plants under water stress. Physiological variables observed were plant growth, plant water status, epicuticular wax production, hormone levels, and photosynthetic capacity for different water stress treatments. The herbicide studies evaluated the effect of water stress on the penetration and activity of two new postemergence sulfonylurea herbicides.

The results from this research will provide a better understanding of physiology for weeds under water stress and the resultant impact on postemergence herbicide activity.

LITERATURE REVIEW

This literature review will describe the current research about shattercane and woolly cupgrass biology, the influence of water stress on plant physiology, experimental techniques used for water stress research, postemergence herbicide/plant interactions, and sulfonylurea herbicide physiology.

Weed Description

Shattercane and woolly cupgrass demonstrate several characteristics of troublesome weeds. Shattercane is an important weed in the North Central States and causes yield reductions in several row crops (Hanway, 1984). Yield reductions have been reported in soybean (Burnside, 1980), corn (Beckett et al., 1988) and sorghum (Vesecky et al., 1973). In areas infested with shattercane, cultivated sorghum species demonstrate a continuous genetic drift toward weedy characteristics due to the cross-pollination between the wild and cultivated biotypes (Klier, 1988).

The success of shattercane as an aggressive weed can be explained by several biological characteristics. Shattercane plants are highly competitive given the tall growth habit and rapid growth rate (Muldoon, 1985). Sorghum plants can produce large numbers of seeds; Burnside

(1984) reported between 500 to 1500 seeds per sorghum panicle. Further, most of the panicles can drop the seeds to the ground (shatter) before crop harvest (Burnside, 1965; Clark and Rosenow, 1968). Shattercane seeds can remain viable for several years when buried in the soil. For example, in some Nebraska soils, shattercane remained viable for 13 years (Burnside et al., 1977).

Woolly cupgrass, an annual grass native to eastern Asia, has not been studied as thoroughly as shattercane. Strand and Miller (1980) described woolly cupgrass as a weed threat in the midwestern agroecosystems, due in part to atrazine tolerance. Also, woolly cupgrass was described as highly competitive in corn (Owen, 1987). The weed is spreading quickly in Iowa and has been identified in 56 counties (Bello, 1988).

Biological characteristics of woolly cupgrass include an aggressive growth habit, prolific seed production, and seed dormancy. Bello (1988) described some biological woolly cupgrass characteristics such as the potential to produce as many as 123,000 seeds, continuous seed germination throughout the growing season, and the presence of primary and secondary seed dormancy.

Plant Physiology under Water Stress

Major crop plants in developed countries exhibit potentially high productivity when grown under ideal environmental conditions. High productivity levels usually are reached for crops grown in monocultures and with highly controlled agronomic inputs such as high fertilization rate, optimal planting date and plant density, and avoidance of weed competition insects and diseases. However, most crop plants are exposed to some degree of unfavorable environmental conditions for growth, thus affecting the real productivity relative to the potential productivity. A number of environmental variables negatively affect plant productivity. Of these, low water availability is the most common and important variable (Boyer, 1982).

When environmental variables such as water are limiting, crop losses occur due to direct and indirect factors. Direct losses of crops due to water stress are mainly expressed as a yield reduction. Crop yield reduction due to drought is a function of three variables: drought duration, drought intensity, and crop phenological stage at the time of water stress. Drought duration and intensity are positively related with productivity losses.

Water stress events demonstrate variable impact depending of the plant species and the specific plant phenological stage at the time of stress.

Indirect losses from water stress are due, in part, to the lack of consistent response of crops and weeds to agronomic practices. Crops do not utilize inputs efficiently and weed management is more difficult under water stress conditions.

Herbicide application to plants affected by water stress results in unpredictable responses. Production costs may increase due to poor herbicide performance thus requiring increased application rates or increased number of tillage operations. Failure in weed control escalates the interspecific plant competition and may increase the future weed seed output. Finally, environmental pollution may increase due to off-target herbicide drift.

Plants respond to water stress through molecular, biochemical, morphological, and physiological changes. When the plant water potential is reduced below a threshold level characteristic for each species, a yet undetermined signal (presumably at the molecular level) activates specific molecular and biochemical responses. Morphological and physiological responses result from the molecular and biochemical precursors.

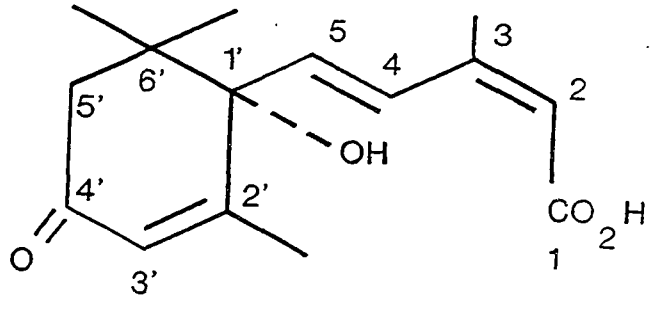
Changes in the shoot/root ratio (Kummerow, 1980), leaf shedding, leaf rolling (Bittman and Simpson, 1989), and leaf angle (Begg, 1980) are among the morphological changes of plants under water stress.

Increases in ABA (Wright and Hiron, 1969), osmotic adjustment (Hsiao and Acevedo, 1973), decreases in the growth rate (Boyer, 1970; Hsiao, 1973), reduced stomatal conductance (Caemmerer and Farquhar, 1981a), reduced photosynthetic rate (Boyer and Bowen, 1970), and increases in epicuticular wax (Skoss, 1955) are the principal physiological changes of plants under water stress.

Cell growth is the plant process most sensitive to water stress and thus altered the first; this is followed by a suppression of cell wall synthesis and cell division. Other processes very sensitive to water stress are protein synthesis and the maintenance of enzyme levels (Hsiao and Acevedo, 1974).

Abscisic Acid

ABA is reported to be an inhibitory compound in higher plants. ABA is a C-15 carboxylic acid containing an unsaturated keto group, a tertiary hydroxyl group, and 2 cis double bonds. A molecule of ABA with the numbering system is shown in Figure 1A. ABA has a single chiral



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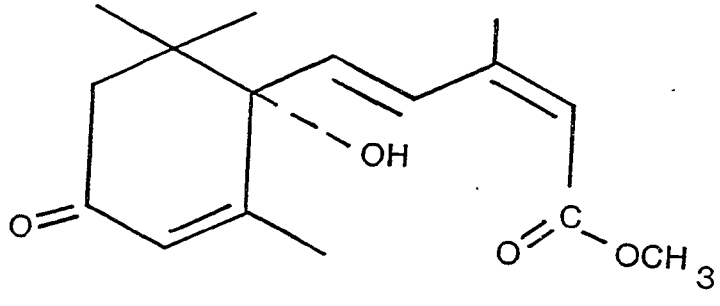

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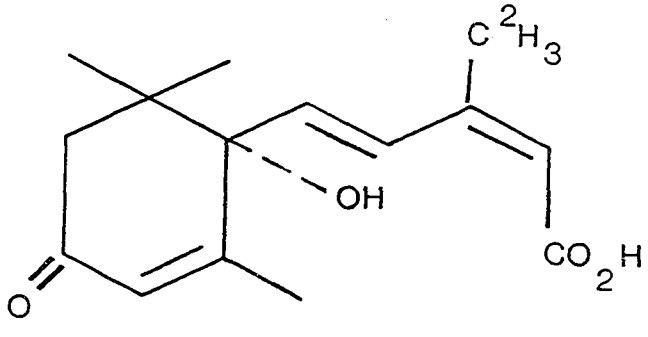

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Figure 1. Chemical structure of ABA and related compounds. A) +(S)-ABA (with the most commonly used numbering system), B) ABA methyl ester, and C) 3-methyl-[^{2}H]-ABA

center at its 1'-carbon which produces two isomeric forms of ABA, but the naturally occurring compound is exclusively the +(S)-enantiomer.

The pathway of ABA synthesis in plants is not yet clear. Mevalonic acid is the primary precursor of ABA. Reviews by Horgan et al. (1983) and Neill et al. (1984) described the two accepted possible pathways of synthesis. One possibility is that ABA is synthesized through a non-carotenoid pathway by cyclization and modification of farnesyl pyrophosphate resulting in ABA that is a sesquiterpene. The other possibility is a carotenoid pathway involving oxidation and reduction of violaxanthin in which case, resulting ABA is an apocarotenoid (Walton, 1980; Zeevaart and Creelman, 1988).

ABA synthesis is likely localized in the cytoplasm of mesophyll cells (Hartung et al., 1981). After synthesis, ABA moves along a pH gradient preferentially to mesophyll chloroplasts that behave like anion traps (Hartung et al., 1982). New evidence suggest that roots tips can synthesize ABA (Cornish and Zeevaart, 1985; Zhang and Davies, 1987). Also, there is a report, although controversial, that guard cells may synthesize ABA (Cornish and Zeevaart, 1986).

ABA and Water Stress

Increased ABA content, in response to water stress, has been described in several species (Wright and Hiron, 1969; Beardsell and Cohen, 1975; Bensen et al., 1988). The effect of ABA on root cell turgor pressure (Jones et al., 1987), hydraulic conductivity of roots (Ludewig et al., 1988; Glinka, 1980), and stomatal control (Jones and Mansfield, 1972; Kondo and Maruta, 1987; Raschke, 1979), is consistent with the theory that ABA appears to modulate the physiological responses of plants under drought stress. During the latter stages of embryogenesis, prior to desiccation, ABA content dramatically increases (King, 1976; Finkelstein et al., 1985). Endogenous ABA levels increase substantially in leaf tissues previously subjected to water stress or wounding (Jones et al., 1987; Walton 1980).

Cowan et al. (1982) suggested that the first response to water stress may be the release of chloroplastic ABA due to reduction in stromal pH, followed by increase in de novo ABA synthesis. Two proposed signals for the ABA biosynthesis have been described; a decrease in mesophyll cell turgor (Pierce and Raschke, 1980) or a decrease in cell size (Hartung et al., 1983). The physiological response of plants under water stress is stomatal closure.

New evidence suggests that after wilting, a sequence of molecular events directs new ABA biosynthesis. Reports suggests that nuclear gene transcription (Guerrero and Mullet, 1986) followed by a rapid induction of mRNA (Bray, 1988; Guerrero and Mullet, 1988) are the molecular precursors of ABA biosynthesis. At the molecular level, it has been demonstrated also that increases in endogenous ABA levels induce the accumulation of specific mRNA and proteins during embryogenesis (Galau et al. 1986), and when plants are under water stress (Jones et al. 1987). ABA-inducible genes have been isolated in rice (Mundy and Chua, 1988) and corn (Gomez et al., 1988) subjected to water stress. The function of the proteins encoded by ABA-inducible genes may be related with some protective function, but is yet not clear (Gomez et al., 1988).

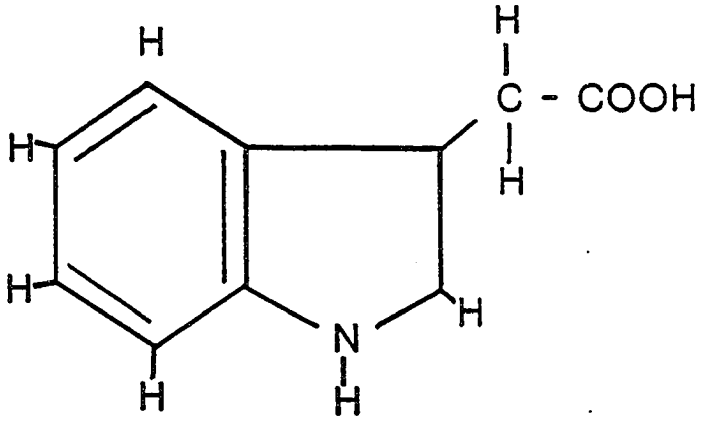
Recent papers describe the possibility that stomatal behavior, leaf growth, and other aspects of shoot physiology are influenced by changes in the edaphic environment surrounding plant roots. Davies et al. (1986) demonstrated that, when part of the root system of corn plants was under water stress, the stomatal conductance decreased with no change in leaf turgor or leaf ABA. The explanation is that changes in the edaphic environment

cause roots to generate chemical signals such as reductions in cytokinin supply (Blackman and Davies, 1985) or increased ABA root production (Zhang and Davies, 1987). The chemical signal is transported to shoots in the transpiration stream and modifies growth or stomatal behavior (Davies et al., 1986). Thus ABA produced in plant roots may be indicative of the soil water status (Turner et al., 1985; Zhang and Davies, 1987; Zhang et al., 1987; Zhang and Davies, 1989).

Further wilting activates genes involved in proline accumulation (Stewart et al., 1986). Proline also accumulates in response to exogenous ABA treatments, and to salt and cold stress. In wilted leaves, ABA accumulation precedes proline accumulation. However, proline accumulation has been shown to be independent of ABA accumulation, suggesting independent sets of gene activation (Stewart and Voetberg, 1987). Other plant hormones such as ethylene, and cytokinins are also involved in the modulation of plant responses to water status (Davies et al., 1986).

Indole-3-Acetic Acid

Indole-3-acetic acid (IAA) is an important plant hormone produced in shoot tips, young leaves, flowers,



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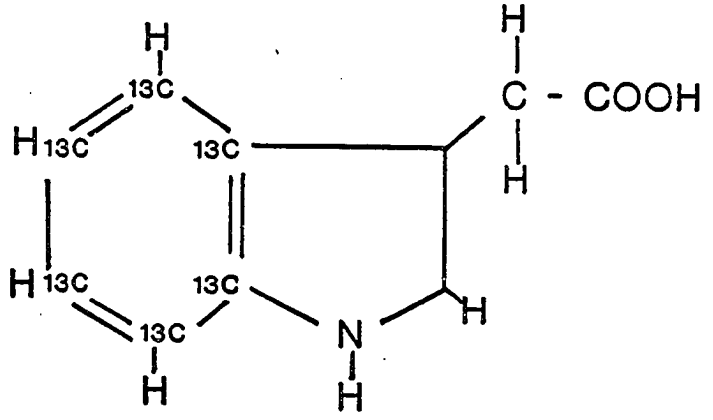

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Figure 2. Chemical structure of IAA. A) indole-3-acetic acid (IAA) and B) carbon-13-labeled IAA ($^{13}C_6$-IAA)

fruits, and seeds of higher plants. Figure 2 depicts the structural configuration of IAA.

The available evidence suggests that tryptophan is the primary precursor in IAA biosynthesis (Bandurski and Nonhebel, 1984). The most common pathway of IAA biosynthesis proceeds from tryptophan and involves the intermediate formation of indole-3-acetaldehyde. Some species are able to convert tryptophan into IAA via tryptamine. Indol-3-acetaldehyde may yield IAA or, by a reversible reaction, may be converted to indole-3-ethanol; this compound is assumed to be a storage form involved in the regulation of IAA synthesis (Sandberg et al., 1987).

IAA catabolism may involve peroxidative processes resulting in the loss of the side chain carboxyl group (decarboxylative catabolism) producing decarboxylated indoles or decarboxylated oxindoles. Non-decarboxylative catabolism of IAA was demonstrated in several species (Bandurski, 1984; Davies, 1973; Epstein et al., 1980). The non-decarboxylative pathway involves an enzymatic step with posterior conjugation (Nonhebel and Bandurski, 1984); several molecules have been described that may conjugate with IAA such as glucose, cellulosic glucan, a glucoprotein, and a polypeptide (Sandberg et al., 1987).

The effect of plant water stress on endogenous IAA concentrations is controversial. Evidence suggest that there is an increase in IAA oxidase activity and a reduction of IAA transport with water deficit (Darbyshire, 1971; Davenport et al., 1977 and 1980; Davies et al., 1986). No reports are available in the literature about IAA synthesis and the simultaneous variation of ABA and IAA under water stress conditions.

Effects of Water Stress on Plant Growth

Plants increase in size mostly by increasing in cell water content. Inhibition of plant cell expansion is one of the earliest detectable responses to water stress (Hsiao, 1973; Rhodes, 1987). Leaf expansion is regarded as one of the physiological process most sensitive to water stress (Boyer, 1970; Hsiao, 1973). Several researchers have reported that plant growth is reduced by water stress conditions (Akey and Morrison, 1984; Hsiao and Acevedo, 1974; Westgate and Boyer, 1985). It is known that leaves senesce under severe water stress (Aparicio-Tejo and Boyer, 1983).

Initial leaf expansion in annual plants demonstrates exponential characteristic. The basic growth mechanisms of leaf initiation, unfolding, and expansion are expression of

the cellular processes of division, expansion, and differentiation (Aspinall, 1986). After cell division occurs, cell enlargement requires water, solute, and turgor. Cell expansion has three components; an increase in cell surface area, an increase in cell volume, and the maintenance of osmotic relations for the cell. Two conditions are fundamental for cell expansion; cell walls must be elastic and capable of irreversible expansion, and the water inside the plant must move preferentially to the growing cell. Increases in cell surface area requires the loosening and extension of cell walls in a very specific way. The volumetric increase of cells is due to water uptake, together with an increase in osmotic content in order to maintain turgor pressure (Tomos, 1985). After the turgor pressure is over a threshold level, cell expansion becomes a linear function of turgor.

Under water stress conditions, leaf initiation and leaf expansion are limited due to effects on cell division and expansion. Further DNA replication is reduced together with protein synthesis and solute accumulation (Aspinall, 1986). It is interesting to note that water relations in expanding leaves are different between monocotyledonous and dicotyledonous plants due to the different growth patterns. Monocot leaves grow from a basal meristem located inside

protective sheath and the leaf bases of older leaves and behave like enclosed tissues during water stress events. If water stress develops in this early stage, leaves exhibit osmotic adjustment. Dicot leaves unfold and expand almost completely in the external environment and water loss occurs immediately after unfolding. Under water stress, expanding leaves of dicot plants do not exhibit osmotic adjustment (Barlow, 1986).

Osmotic Adjustment

Osmotic adjustment is the ability of plant cells to regulate the amount of internal solute molecules, thus decreasing osmotic potential. The resulting lower water potential drives water uptake to maintain turgor and cell volume in response to water stress or salinity. Osmotic adjustment is a recognized plant cell response (Morgan, 1984; Wyn Jones and Gorham, 1986; Shackel and Hall, 1983).

In lower organisms, potassium ions are the primary osmolyte, and potassium ion accumulation permits the balancing of external osmolarity together with maintenance of turgor. Potassium is an appropriate osmolyte because it is ubiquous in the environment, but excessive accumulation of this ion may inhibit enzyme activity. Osmotic regulation (accumulation of intracellular solutes), is

observed in higher plants. However, solutes compatible with normal metabolism and enzyme activity are produced and accumulated such as: sugars, sugar alcohols, betaine, and proline (Wyn Jones and Gorham, 1986; Higgins et al., 1987). Osmotic adjustment in sorghum has been well documented, especially when the water stress increases slowly (Begg and Turner, 1976; Ferreres et al., 1978; Jones et al., 1980; Jones and Rawson, 1979; Jones and Turner, 1978; McCree et al., 1984; McCree, 1986; Turner et al., 1978).

Photosynthesis and Water Stress

Water stress also affects the rate of photosynthesis (Boyer and Bowen, 1970). Under water stress, the CO_2 exchange is altered by reductions in stomatal aperture and changes of CO_2 diffusion resistance in the mesophyll cells. Under drought stress, decreases in the stomatal conductance decreases the transpiration rate and thus avoiding low leaf water potentials. Stomatal closure induced by water stress decreased photosynthetic assimilation by 20 to 25% (Farquhar and Sharkey, 1982).

Decreased photosynthetic assimilation under water stress conditions can also be due to nonstomatal inhibition of photosynthesis (Hsiao, 1973). The photochemical components of the photosynthetic apparatus are more

sensitive to water stress than the enzymatic apparatus (Kriedemann and Downton, 1981). Plants under water stress may demonstrate nonstomatal inhibition of photosynthesis due to a photoinhibition mechanism that ultimately causes damage to the photosynthetic machinery of the chloroplast (Powles, 1984). A relationship between photosynthesis rate and decreasing leaf water potential was reported by Boyer (1976).

Stomatal Conductance

Stomatal function influences two basic physiological functions, transpiration rate and rate of carbon dioxide movement into the leaf, thus influencing plant growth and productivity (through modulation of CO_2 exchange and plant water status). In turn, changes in transpiration rate may modify leaf water potential and leaf temperature. Leaf stomata respond to environmental and internal conditions in a very complex way (Hall and Schulze, 1980). Stomatal conductance is affected by light, CO_2 concentration, the vapor pressure difference between leaf and environment, leaf water content and leaf temperature (Caemmerer and Farquhar, 1981a; Cowan, 1977).

Stomatal closure is associated with changes in the turgor of guard cells under environmental stress and is affected by water stress (Kondo and Maruta, 1987).

Plant Epidermis

The epidermal cell layer of higher plants is covered by a continuous cuticle, hydrophobic in nature, and composed of three layers. The basal layer adheres to the middle lamella of the epidermal cells and is a mix of cutin, wax, cell-wall polysaccharides, and proteins. The middle layer is a matrix of cutin with embedded wax and the surface layer is made primarily of epicuticular wax deposited on the cutin surface. The ultrastructure of the epicuticular wax varies from amorphous to highly crystalline deposition. Generally, wax distribution on the leaf surface is not uniform; epicuticular wax deposition is thin or nonexistent above veins, leaf margins, guard cells, and leaf hairs. Pectin strands permeate the cutin matrix. The pectins are a group of polysaccharides. The most abundant component of the pectin polysaccharides are polyuronic acids. Pectins are the most hydrophilic cuticle components followed by cutin, while waxes are the most hydrophobic cuticle components.

Cutin is a polyester of hydroxylated fatty acids, usually 16 or 18 carbon chain lengths, organized in a three-dimensional network. The epicuticular wax is composed of a complex mixture of long-chain aliphatic and cyclic compounds. Major constituents of epicuticular wax are esters of fatty acids and long chain alcohols (C_{26}, C_{28},

C_{30}), free long chain fatty acids, free long chain alcohols, and long chain alkanes and ketones (Chamel, 1988).

The chemical composition of the epicuticular wax and the nature of the chemical groups exposed at the surface, influences the wetting and retention characteristics of the cuticle. In general, waxes with long-chain ketones and alkanes are the most difficult to wet.

Cuticles and Water Stress

Plant species, environmental conditions during cuticle deposition, and plant age determine the relative proportion and composition of wax, pectin, and cutin in the cuticle. Several workers have reported a correlation between environmental variables and cuticle composition. Water stress (Skoss, 1955), low relative humidity (Baker, 1974), temperature (Hull et al. 1975), and light intensity (Skoss, 1955) all affect differential cuticle composition and structure. Svenningsson, in 1988, demonstrated changes in oat (Hordeum vulgare L.) epi- and intracuticular lipids composition; additionally, cuticular transpiration rates were altered under water stress, but no relation between both variables were found.

Epicuticular wax load increased in plants under water stress (Skoss, 1955; Jordan et al., 1983). The main effect of extra epicuticular wax deposition may be related with

decreasing cuticular transpiration, increasing radiation reflectance, or thickening the boundary layer. The practical result must be reduced total water loss under water stress.

Biosynthesis of epicuticular waxes are additionally affected by environmental conditions (Baker, 1974), plant age (Wilkinson and Kasperbauer, 1972), and pesticide treatments (Ebert and Ramsteiner, 1984; Wilkinson, 1974).

Under normal conditions cuticles offer the greatest resistance to the movement of pesticides into plants. Under water stress conditions, cuticles are modified, increasing the fore mentioned resistance.

Methods to Generate Water Stress

An adequate method for generating water stress must be capable of producing a repeatable range of water stresses. Krizek (1985) described four main experimental methods to develop water stress in plants: a) regulating the timing and/or amount of water given to the plant (Shantz, 1925; Veihmeyer, 1927), b) incorporation of an osmoticum into the growing medium (soil or water culture) to manipulate the water potential of the medium (Painter, 1966), c) incorporate an osmoticum to manipulate the osmotic or matric potential of the growth medium using a semipermeable membrane to avoid direct contact of the

osmoticum with the roots (Tingey and Stockwell, 1977; Zur, 1966), and d) use water columns of varying height (Snow and Tingey, 1985).

The methods in which specific amounts of water are added to the growing media have several restrictions. With small pot sizes, uneven water distribution is obtained, root volumes are limited, and drought development is usually rapid. This rapid drought development results in plants that do not demonstrate proper osmotic adjustment. However, these methods permit the use of large numbers of plants. With larger pot sizes, roots may be maintained at different levels of water stress, but the total number of plants that can be handled simultaneously is greatly reduced (Pennypacker et al., 1990).

Methods that use osmotica in direct contact with roots, i.e., polyethylene glycol (PEG) may have problems associated with plant toxicity, interference with normal mineral nutrition such as reduced phosphorous uptake, or direct absorption of osmoticum by plants roots (Snow and Tingey, 1985). The addition of NaCl to the growth media may cause salinity stress. Semipermeable membranes that separate plant roots from the soil solution with the osmoticum, significantly restrict available root volume, and are easily degraded by soil microorganisms (Tingey and

Stockwell, 1977). Finally methods that control water potential with water columns of known height are very complex to operate or duplicate.

Further details of the theoretical ideas behind plant water relations, and the practical implications of measurements of plant water status used in this work, can be found in several works (Barrs, 1968; Boyer, 1969; Slavik, 1974; Turner, 1981).

Herbicides

Herbicide Development

The development of new pesticides requires the optimization of several criteria such as high selectivity and reliability against the target organism, cost effectiveness, the avoidance of harmful environmental effects, and low toxicity in mammals, birds, bees, and fishes. The discovery of new herbicides follows three classical patterns: a) random screening of chemicals, b) the use of known herbicides as lead compounds for a synthesis program, and c) the rational design of compounds based on knowledge of metabolic processes and modes of action. Until now, the two initial approaches are responsible for the discovery of most pesticides used in world agricultural production. The rational approach is

used for further development of pesticides and formulations.

Herbicides require a transfer process from the point of application to the receiving organism, followed by penetration and transport to the active site before plant toxicity can develop. Additionally, chemical modification often occurs within the target organism. Thus the final toxic effect of the chemical agent is determined by the magnitude of the vital process that it affects and the amount of substance that reaches the action site (Graham-Bryce, 1984).

In most pesticide treatments, only a very small percent of the applied dose causes the intended effect due to weathering, inactivation, and redistribution processes. This low efficiency is difficult to improve under actual use conditions (Graham-Bryce, 1984). Figure 3 shows the fate of a postemergence herbicide from the point of atomization to the final biological effect.

After herbicides are deposited on the target surface, a critical concentration of intact and active molecules must be transported to the active site. Herbicides are subjected to several partitions between different polarity phases on the pathway from the external cuticle to the target site (Hansch and Fujita, 1964).

Postemergence Herbicides

The use of postemergence herbicides is increasing, specifically in no-till production systems and for the control of problem weeds. More herbicides for postemergence use have become available in the market during the last decade (Wanamarta and Penner, 1989). The presence of Sorghum spp. and Eriochloa spp. represents a problem in areas with obligate corn rotation, due to the lack of adequate control strategies. Nicosulfuron, 2-[[(4,6-dimethoxypyrimidin-2-yl)aminocarbonyl]aminosulfonyl]-N,N-dimethyl-3-pyridinecarboxamide, and primisulfuron-methyl, 3-[4,6-bis-(difluoromethoxy)-pyrimidin-2-yl]-1-(2-methoxycarbonylphenylsulfonyl)urea, are new sulfonylurea postemergence herbicide products for corn, with activity in grasses and broadleaves (Maurer et al. 1987).

The biological activity of postemergence herbicides is affected by physico-chemical and biophysical properties of the herbicide and the spray solution, by the morphological state of the plant, and by the environmental conditions during application time (Gerber et al., 1983; Kudsk et al., 1990).

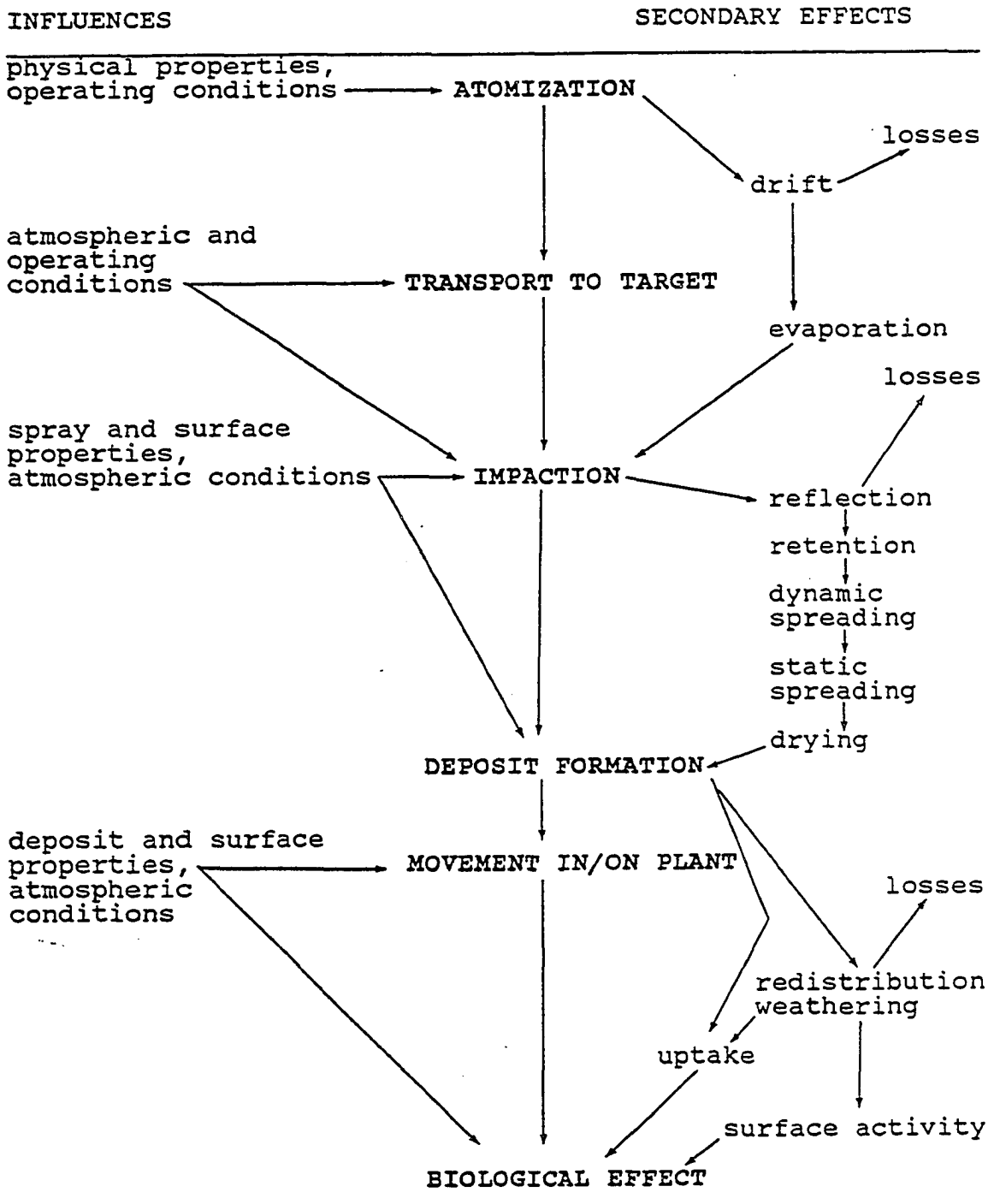


Figure 3. Component interdependency between spray application and biological effects (Hall, 1988)

Effect of Water Stress on Postemergence Herbicide Activity

Reduced effectiveness of postemergence herbicides on plants under water stress has been reported from field, greenhouse, and growth chamber studies (Chernicky et al., 1984; Jeffcoat et al., 1977; Kells et al., 1984; Kloppenburg and Hall, 1990; Miller et al., 1978). The proposed mechanisms that may account for reduced herbicide activity on water stressed plants are related with alterations of herbicide retention, absorption, translocation, or metabolism (Shahi, 1975). Studies with herbicides used for broadleaf weed control demonstrated that water stress interferes with the normal retention, absorption, and translocation of the herbicide (Willingham and Graham, 1988). Several reports described the reduced activity of some selective postemergence grass herbicides on plants under water stress (Akey and Morrison, 1983; Dastgheib et al., 1990; Kidder and Behrens, 1988; Peregoy et al., 1990). Diclofop-methyl [(±)-2-[4-(2,4-dichlorophenoxy)phenoxy]propanoic acid], has been found to be less effective against wild oat [Avena fatua (L.)] grown under low soil moisture conditions. Uptake and translocation of the herbicide were not significantly reduced under drought conditions (Akey and Morrison, 1983). Strong evidence that demonstrates differential

translocation of postemergence grass herbicides in plants under water stress is lacking, however, less extensive distribution of herbicides in plants growing under water stress was reported (Akey and Morrison, 1983; Kells et al., 1984).

Weeds affected by water stress demonstrate a reduced response to glyphosate [N-(phosphonomethyl)glycine]. Decreased absorption and translocation accounted for this reduced effectiveness (Ahmadi et al., 1980; Chase and Appleby, 1979; Waldecker and Wyse, 1985).

No information is available describing the interaction between nicosulfuron and primisulfuron-methyl with shattercane and woolly cupgrasas grown under water stress conditions.

Foliar Absorption of Postemergence Herbicides

Penetration into plants requires that the herbicide molecules permeate cuticles, cell walls, and plasmalemma. However, the herbicide must be readily available at the plant surface; photochemical stability and a low vapor pressure are desirable postemergence herbicide characteristics. Uptake rate during the droplet drying period has been shown to be 100 to 1000 times faster than from dry spray deposits (Stevens et al., 1988). Leaf

epicuticular waxes are the primary barrier to herbicide movement from the external area of impact to the internal plant tissue (Dan Hess, 1985). Kirkwood (1987) demonstrated that asulam (methyl[(4-aminophenyl)sulfonyl] carbamate) absorption was influenced by tissue age and epicuticular wax. If the herbicide remains on the epicuticular surface (external retention), it can be lost by volatilization, crystallization, or subsequent rain washing. Adjuvants are frequently used to help optimize herbicide penetration and thus biological performance. Sometimes the herbicide can penetrate into the cuticle, but remains associated with cuticle components (cuticular retention) (Wanamarta and Penner, 1989).

Herbicide movement across the cuticle is a simple diffusion process, via aqueous routes for polar materials, and via lipoidal routes for nonpolar materials. Nonpolar molecules are taken up by sorption into the epicuticular wax, passing through the cuticle, and demonstrate apoplastic desorption into the cell wall. Polar molecules move easily through hydrated cuticles. However, under water stress, it has been suggested that polysaccharide microfibrils that extend from the cell wall to the cuticle surface are the hydrophilic pathway for herbicide movement (Stevens and Baker, 1987; Wanamarta and Penner, 1989).

However, Baker and Hunt (1988) suggested that if polar routes exist through the cuticle, they are very inefficient.

After the cuticular penetration, herbicides must move through the cell wall and the plasmalemma. The cell wall offers little resistance to herbicide penetration and diffusion is the main mechanism of penetration. Theories of plasmalemma penetration by herbicides include simple diffusion, or the use of carrier molecules with energy expenditure (Devine, 1989; Wanamarta and Penner, 1989).

Uptake of herbicides through apoplastic compartments are associated with median hydrophobicity. The hydrophobic parameter, log P (P is the partition coefficient of octanol/water) has an optimal value between 2.0 and 2.5 for plants. Under such log P values, there is an increase of solvation forces which compete in the aqueous and the lipid phase, resulting in optimal uptake (Leo, 1984). Molar water solubility (log S) has an optimal value for foliar uptake between -1.5 to -3.5 (Baker and Hunt, 1988). Experiments demonstrate that herbicide uptake is optimal for compounds of intermediate lipophilicity [log P 2.0 to 2.5 and log S -1.5 to -3.5] (Baker and Hunt, 1988; Chamberlain et al., 1987; Kirkwood, 1987).

Entry into the symplasm occurs by simple diffusion, or by carrier transport. Simple diffusion is governed by

Fick's first law, with more lipophilic herbicides penetrating membranes more rapidly than less lipophilic compounds. According to Fick's first law, the rate of diffusion across a membrane is proportional to the concentration gradient across it. Active uptake of herbicides by a carrier-dependent mechanism was only proved for 2,4-D [(2,4-dichlorophenoxy)acetic acid] and glyphosate [N-(phosphonomethyl)glycine] (Devine, 1989).

Uptake of pH neutral herbicides is not influenced by external pH, but the uptake of weak acid herbicides is pH dependent, with greater uptake at lower pH. At a low pH, such as the pH in cell walls, these herbicides are preferentially undissociated, with a more lipophilic affinity, showing high membrane permeability (Devine et al., 1987).

Herbicide Transport

After herbicides enter plants, translocation may occur from the site of entry to other tissues. The need for phloem transport is greatest for those herbicides that interfere with processes occurring at meristematic areas (Devine and Vanden Born, 1985; Lichtner, 1986). Herbicides translocate with plant assimilates, typically from leaves to regions of new growth. This process is described as

herbicide movement from source to sink. Phloem transport of molecules has three components; phloem loading, phloem transport, and phloem unloading. Herbicide loading and unloading processes may occur by diffusion or active mechanisms as explained above. Phloem transport is by mass flow (Cronshaw et al., 1986).

After herbicides enter the symplasm, they may be retained by several mechanisms. The first theory that explained phloem mobility of pesticides is called the weak acid theory (Crisp and Look, 1978). Weak acid herbicides dissociate inside the symplasm due to the higher pH, resulting in molecules that are less lipophilic, and thus less membrane permeable. This dissociation results in acid trapping, where acids are accumulated in alkaline compartments.

The second theory, called the intermediate permeability hypothesis, states that phloem mobility is controlled by the permeability coefficient of the compound (Tyree et al., 1979). Molecules with high membrane permeabilities, have little net phloem movement, and molecules with low membrane permeabilities are slowly absorbed into the symplasm, but are retained there due to low permeability. In between these permeability extremes

are molecules with optimum (intermediate) permeability, for absorption and transport.

Two physico-chemical parameters are important in explaining herbicide transport: the dissociation constant (pK_a) and the hydrophobic parameter (log P) of herbicides. Herbicides that have functional groups capable of ionization in the symplasm, together with a change in molecule lipophilicity, will most likely be retained and translocated in the symplasm. Optimal log P for herbicide translocation is between 2.0 to 2.5. The rate of phloem translocation of assimilates and herbicides depends in part on the rate of photosynthesis which is under environmental control.

Studies of retention, uptake, transport, and metabolization of herbicides are currently being developed with the combined use of radioactive herbicides and radioisotope techniques (Corbin and Swisher, 1986; Devine, 1989).

Sulfonylurea Herbicides

Sulfonylurea herbicides are relatively new compounds. The first patent was accepted in 1977. The evolution of agrochemical concepts is clearly described and summarized by this herbicide family: new herbicide products that

exhibit high specificity and significant activity at low dosage with reduced environmental impact, low human and animal toxicity. Today, sulfonylureas are responsible for one of the largest herbicide research programs in the history of the agrochemical industry due to potent biological activity and countless possibilities for the generation of new products (Beyer et al., 1988, Sauers and Levitt, 1984). Several compounds from this family are commercialized products in the United States and in the world for different crops and weeds.

Biologically, sulfonylureas are potent inhibitors of plant growth through inhibition of plant cell division (Ray, 1982). Plant death is slow and is accompanied by chlorosis, necrosis, terminal bud death, and total inhibition of plant growth. Photosynthesis and respiration are not initially affected by herbicide action (Ray, 1982).

The mode of action of these herbicides was first determined in several bacteria species. Results indicated that the herbicide activity is through the inhibition of the enzyme acetolactate synthase (ALS) (EC 4.1.3.18) or acetohydroxyacid synthase (AHAS) (LaRossa and Schloss, 1984; Ray, 1984; Rost and Reynolds, 1985). ALS/AHAS is a very unusual enzyme and is the key enzyme in the biosynthetic pathway leading to the formation of branched

chain amino acids L-valine, L-leucine, and L-isoleucine. The accepted theory suggests that sulfonylurea molecules binds to the ALS-FAD-TPP-Mg^{+2}-decarboxylated pyruvate complex and competes for the second pyruvate binding site (Beyer et al., 1988). Ray (1984), and Chaleff and Mauvais (1984), reported a similar site of action for sulfonylureas in higher plants. However, the plant enzyme was significantly more sensitive that the bacterial ALS enzyme. The concentration of sulfometuron methyl (methyl-2-[[(4,6-dimethyl-pyrimidin-2-yl)aminocarbonyl]-aminosulfonyl] benzoate) in nanomoles (nM) required to inhibit ALS by 50% (I_{50}) was 65 for bacteria, 15 for pea, and 7 for wild oats (Chaleff and Ray, 1984; LaRossa and Schloss, 1984).

An important point in the development of sulfonylureas was the understanding of the mechanism of selectivity and resistance in different crops. Plants resistant to sulfonylureas contain an altered ALS enzyme (Chaleff and Ray, 1984). Tolerance to sulfonylurea herbicides is achieved by detoxification mechanisms (Hutchison et al., 1984; Sweetser et al., 1982). Selectivity to sulfonylureas can be explained by differential metabolism between crops and sensitive weed species (Anderson et al., 1989; Brown et al., 1990; Brown and Neighbors, 1987).

A frequent pattern of sulfonylurea metabolism is by introduction of hydroxyl functions (in different places of the structure), followed by carbohydrate conjugation. Sweetser et al. (1982) demonstrated that chlorsulfuron (2-chloro-N-[[(4-methoxy-6-methyl-1,3,5-triazin-2-yl)amino]carbonyl]benzenesulfonamide) is metabolized by aryl hydroxylation in wheat [Triticum aestivum (L.)], whereas hydroxylation on the triazinyl methyl group was reported in black nightshade Solanum nigrum (Hutchison et al., 1984). Brown and Neighbors (1987) reported the conjugation of chlorimuron ethyl (2-[[[[4-chloro-6-methoxy-2-pyrimidinyl]amino]carbonyl]amino]sulfonyl]benzoic acid) to homoglutathione in soybeans [Glycine max (L.)]. Beyer et al., (1988) described the chemical and biological rules for sulfonylurea tolerance as the appearance of a "metabolizable" site in the molecule, fast metabolism with a half-life of only a few hours, and the generation of metabolic products with greatly diminished herbicide potency.

Sulfonylureas are phloem mobile molecules and weak acids thus primarily exist in the protonated state at low pH. The effect of pH on the log P coefficient is opposite to its effect on water solubility. As pH increases, more sulfonylurea molecules exist in the anionic form, decreasing

partitioning into octanol. Uncharged molecules are more lipophilic than the anionic form (Lichtner, 1986). Postemergence applied sulfonylurea herbicides must be incorporated into the symplast of the plant. When sulfonylurea molecules reach the acidic cell wall (apoplast pH = 5.5), many molecules are in the neutral, permeable form, and are able to cross the plasma membrane and enter the phloem. Inside the phloem sap (symplast pH = 8.0), molecules dissociate, and become impermeable and are trapped in the symplasm (acid-trapping mechanism). Movement of herbicide molecules in the phloem is by mass-flow together with sucrose and other solutes (Lichtner, 1986). Bestman et al. (1990) reported a decrease in assimilate transport of field pennycress (Thlaspi arvensis) after chlorsulfuron application. One possibility suggested was that the herbicide action may be associated with the depletion of proteins involved in sucrose transport into the phloem.

Usually sulfonylurea compounds present low acute oral, dermal and inhalation toxicities in mammals. Also, no mutagenic and teratogenic activity was reported for this chemical family. Subchronic feeding, chronic feeding, and reproductive studies are very favorable. The toxicity for

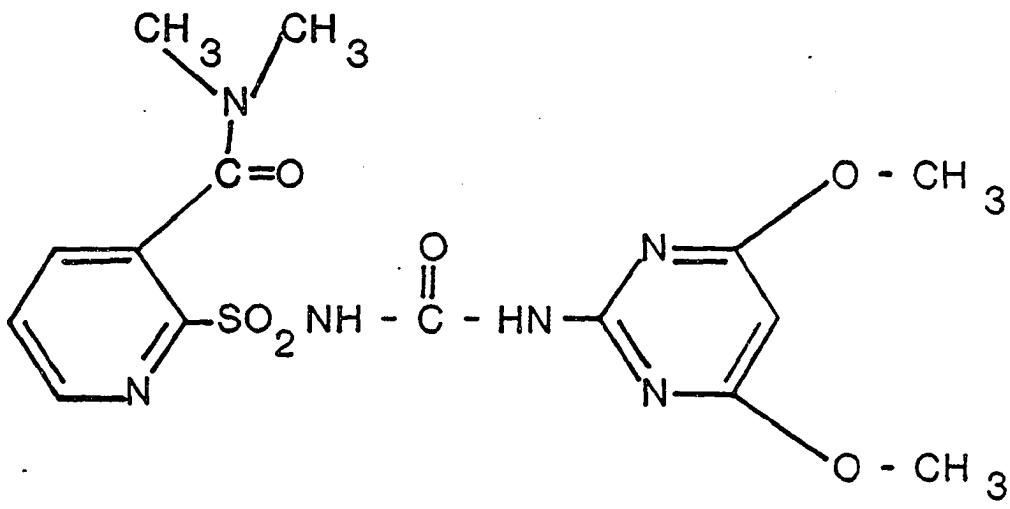
fish, wildlife, and honey bees is low (Beyer et al., 1988). Sulfonylurea compounds were originally derived from triazine compounds. The general sulfonylurea molecule is composed of three different parts; an aryl group, the sulfonylurea bridge, and a nitrogen-containing heterocycle. Different chemical substituents in different positions of a sulfonylurea molecule give innumerable possibilities for the development of new active compounds.

New sulfonylurea herbicides have been developed for grass control in corn [Zea mays (L.)] (Kuratle et al., 1988; Porpiglia et al., 1988). The new compounds have interesting characteristics such as significant biological selectivity, high herbicidal activity, and notable toxicological safety. Corn tolerance is attributed to herbicide metabolism to nontoxic products. These herbicides are used at very low application rates and have low acute oral, dermal and inhalation toxicities in mammals.

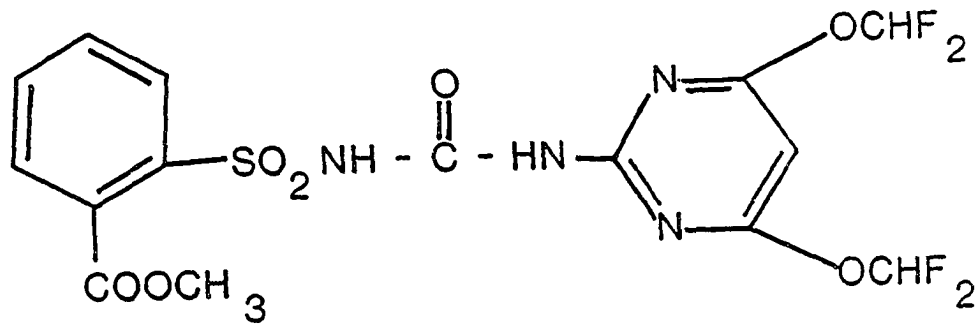
Two postemergence herbicides for grass control in corn were studied: nicosulfuron, formerly DPX-V9360, and primisulfuron-methyl, formerly CGA-136872. Figure 4 displays the chemical structures of both compounds.

Some relevant physical and chemical characteristics of these compounds are tabulated in Table 1. Some toxicological and degradation characteristics of these herbicides are shown in Table 2.

Selectivity of nicosulfuron and primisulfuron-methyl in corn has been associated with the ability of the crop to rapidly convert the products into inactive products. The half-life of primisulfuron-methyl in corn is 5 h. Primisulfuron is metabolized in corn by hydroxylation and subsequent sugar conjugation of the phenyl and pyrimidine ring (Madrid et al., 1988). Fonne-Pfister et al. (1990) demonstrated that primisulfuron-methyl is metabolized in corn by a cytochrome P450-dependent monooxygenase system located in the microsomal fraction. No similar information is available about nicosulfuron metabolization.



NICOSULFURON



PRIMISULFURON-METHYL

Figure 4. Chemical structures of nicosulfuron and primisulfuron-methyl

Table 1. Selected physical and chemical characteristics of nicosulfuron and primisulfuron-methyl (Ciba-Geigy, 1989; DuPont, 1989)

	NICOSULFURON	PRIMISULFURON-METHYL
PHYSICAL STATE	Solid	Crystalline
MELTING POINT	141-144 C	203 C
VAPOR PRESSURE	1.2×10^{-16} mm Hg	$<7.5 \times 10^{-12}$ mm Hg
DISSOC. CONST. (pK_a)	4.3	5.1
OCTANOL/WATER PARTITION COEFFICIENT AT pH 7	0.018	0.059
WATER SOLUBILITY	Buffered water	Water
AT pH 5	360 ppm	1 ppm
AT pH 7	12200 ppm	70 ppm
AT pH 9	39200 ppm	4500 ppm

Table 2. Selected toxicological and degradative characteristics of nicosulfuron and primisulfuron-methyl (technical products). (Ciba-Geigy, 1989; DuPont, 1989)

	NICOSULFURON	PRIMISULFURON-METHYL
ACUTE TOXICITY		
Oral LD_{50} (rat)	>5000 mg/kg	>5050 mg/kg
Dermal LD_{50} (rabbit)	>2000 mg/kg	>2010 mg/kg
Inhalation LD_{50} (rat)	>5.9 mg/L	>4.8 mg/L
SUBCHRONIC TOXICITY		
Oral (90 days feeding Rat, mouse, dog)	NOEL[a] 20000 ppm	NOEL 10000 ppm
CHRONIC TOXICITY		
2-year rat	NOEL 20000 ppm	n.a.[b]
18-month mouse	NOEL 7500 ppm	n.a.
MUTAGENICITY		
Several test	Not mutagenic	Not mutagenic
TERATOGENICITY		
Rats and rabbits	Not teratog.[c]	Not teratog.
GENERAL TOXICITY		
Toxicity Category	III	III
Signal word	Caution	Caution
SOIL METABOLISM AND DEGRADATION		
Degradation	Hydrolysis	Hydrolysis
Half-life	19 to 100 days	21 to 70 days
Soil mobility	Low to intermediate	n.a.

[a]NOEL (no observable effect level).
[b]n.a. (data not available).
[c]Teratogenic.

SECTION I. EFFECT OF WATER STRESS ON PHYSIOLOGICAL PARAMETERS OF SHATTERCANE (Sorghum bicolor [L.] Moench) AND WOOLLY CUPGRASS (Eriochloa villosa [Thunb.] Kunth)

Introduction

Modern agricultural production relies on the correct combination of crops, environmental variables, and agronomic technologies. Water is the environmental resource most limiting to crop production in the United States. A quarter of the total agricultural area of the United States has soils with some degree of water limitation. Similar data apply to the world soils (Boyer, 1982).

Metabolic changes in plants caused by water stress are reduced plant growth (Boyer, 1970; Hsiao, 1973), inhibited cell elongation (Hsiao and Acevedo, 1974), reduced photosynthesis (Boyer and Bowen, 1970), decreased nutrient uptake, and altered balance of hormone levels (Wright and Hiron, 1969; Davies et al., 1986).

Experimental procedures that subject plants to water stress must accommodate reproducible drought intensity and duration. Two commonly used techniques to generate water stress in pots are based on the addition of a precise

amount of water through irrigation (Shantz, 1925; Veihmeyer,1927), or by controlling the external osmoticum potential using semipermeable membranes (Zur, 1966; Painter, 1966). Both systems present problems related to uneven soil wetting, in the case of irrigation systems (Kramer, 1983), or microbial decomposition of the semipermeable membranes (Tingey and Stockwell, 1977).

Shattercane and woolly cupgrass are two economically important weeds in Iowa that are increasing in geographical distribution. Both grasses demonstrate remarkable weedy characteristics such as rapid growth rate, high reproductive capacity, seed dormancy, and are difficult to control with conventional methods.

Shattercane is a serious weed in the North Central States and reduces yield in several row crops (Beckett et al., 1988; Burnside, 1980; Hanway, 1984; Vesecky et al., 1973). In areas infested with shattercane, cultivated sorghum species demonstrate evidence of a continuous genetic drift toward weedy characteristics due to cross-fertilization between the wild and cultivated biotypes (Klier, 1988).

The success of shattercane as a major weed can be explained by several biological characteristics. Sorghum plants are highly competitive due to a tall growth habit

and high growth rate (Muldoon, 1985). Shattercane plants can produce a large number of seeds. Burnside (1984) reported seed production of 500 to 1500 seeds per sorghum panicle. Further, most of the panicles can release the seeds (shatter) before crop harvest (Burnside, 1965, Clark and Rosenow, 1968). Shattercane seeds can remain viable for several years in the soil. In some Nebraska soils, shattercane remained viable for 13 years (Burnside et al., 1977).

Woolly cupgrass, an annual grass native to eastern Asia and introduced into the United States, is a weed less studied than shattercane, but has been reported by Strand and Miller (1980) as a threat to the midwestern agroecosystems, due to demonstrated atrazine tolerance. Also, woolly cupgrass was described as highly competitive in corn (Owen, 1987). The weed is spreading quickly in Iowa and has been identified in 56 counties (Bello, 1988).

Biological characteristics of woolly cupgrass include an aggressive growth habit, prolific seed production (potential production of 164,000 seeds per plant), seed dormancy, and seed germination continuous throughout the growing season (Bello, 1988).

Shattercane and woolly cupgrass are difficult to control and tenacious weeds. Successful management

programs require more complex strategies that include crop rotation, use of specific herbicides, and cultivation. These management systems generally have higher production costs than systems for other annual grass weeds.

The objective of this study was to evaluate physiological parameters for shattercane and woolly cupgrass subjected to different degrees of water stress. Plant growth, plant water potential, stomatal conductance, photosynthetic activity, epicuticular wax content, ABA and IAA levels were determined. Anatomical observations were made of the leaf surface, together with internal morphological differences of leaves subjected to different levels of water stress.

Materials and Methods

General Procedures

Individual plants were grown in 500 cm^3 plastic pots filled with 450 g of air dried composite growth media [80:20 (v/v) of soil and sand]. Three shattercane or woolly cupgrass seeds were planted in each pot and, three days after emergence, plants were thinned to one plant/pot. The seed sources were natural populations of shattercane from Dallas Center, Iowa, and woolly cupgrass from Stratford, Iowa.

The soil moisture characteristic curve for the growth media was determined with a tension table in the low suction range (0.0001 to 0.1 MPa) and with a ceramic pressure plate apparatus in the high suction range (0.1 to 1.5 MPa). The desorption data were used to solve the Van Genuchten equation thus describing the relationship between matric potential and the volumetric soil water content (Van Genuchten, 1980), using the nonlinear regression (NLIN) procedure of SAS (SAS Institute Inc, Cary, North Carolina). Figure 5 shows the volumetric soil water content as a function of the matric suction of the growth medium.

Soil moisture was maintained at field capacity during the initial 21 days after weed emergence using a drip irrigation system. After day 21, plants were separated into four blocks and each block was randomly assigned to one of the four levels of soil water potential. The four levels of soil water potential were maintained for 9 days. Soil water stress treatments were: -0.03, -0.4, -0.8, and -1.2 MPa. Pots were weighed twice daily and water was added with a syringe equipped with a 10 cm long needle

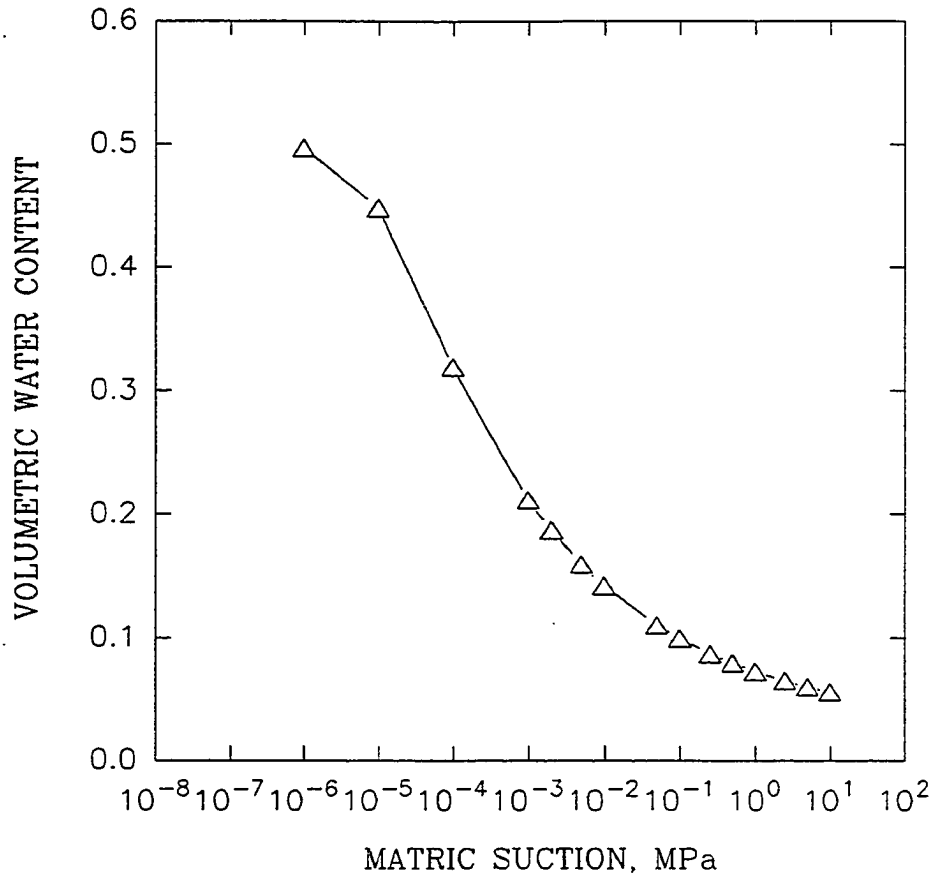


Figure 5. Volumetric water content plotted as a function of the matric suction of the growth medium

containing lateral perforations that allowed even distribution of water in the soil profile.

Pots were maintained during the experiment period in growth chambers (CW 36 Conviron Products Co., Winnipeg, Manitoba, Canada) set for 16 h light/8 h dark.

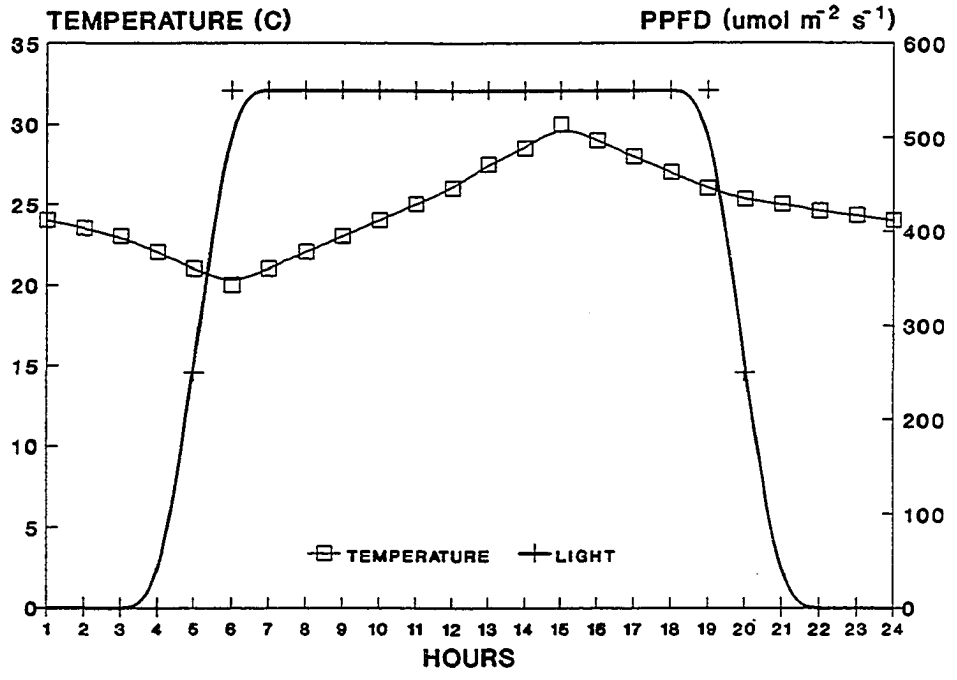


Figure 6. Daily variation of temperature and photosynthetic photon flux density (PPFD) in the growth chamber

Photosynthetic photon flux density (PPFD) at the top of the canopy was 500 μmol m^{-2} s^{-1} and provided by a combination of fluorescent and incandescent lamps. The relative humidity was maintained at 85%. The daily course of temperature and PPFD is shown in Figure 6. Plants were fertilized weekly with 40 ml of a solution containing 3.1 g fertilizer/L of 20-20-20 ($N-P_2O_5-K_2O$) (W. Grace & Co-Conn., Fogelsville, PA).

Electron Microscopy

Fresh pieces (1 cm^2) of the last fully expanded leaves of shattercane and woolly cupgrass were excised, adhered to a brass stub, and the cut margins were immediately sealed with colloidal silver adhesive thus avoiding tissue dehydration. Samples were sputter coated with gold-palladium in a sputter coater (Polaron Instruments Inc., Model E5100) and immediately placed in the scanning electron microscope (SEM) (JEOL-ISM 35) chamber for epicuticular wax observation and photography. The SEM was operated at 15 kV.

A second technique used was cryo-SEM. Small pieces of the last fully expanded leaves of both weeds were excised, adhered to specimen holders, and immediately frozen in liquid nitrogen slush (Emscope cryo system SP 2000 A). Samples were then fractured, sputter coated with gold-palladium and transferred to the SEM chamber that was maintained near liquid nitrogen temperature. This technique was used to observe internal morphological differences in transverse sections of fresh fractured leaves subjected to different levels of water stress.

Growth Characterization

Plant growth was characterized by direct measurements of 2 primary growth variables; total leaf area and total dry weight. These data were used to derive other growth parameters (Hunt, 1982; Hunt, 1990). The derived parameters were mean leaf area expansion rate (MLAER) (Nelson and Sleper, 1981; Radosevich and Holt, 1984), relative growth rate (RGR) (Watson, 1958), and mean growth rate (MGR) (Radford, 1967). These parameters describe the rate of change of leaf area and dry matter production per unit of area, respectively.

In an initial study using only well-watered shattercane and woolly cupgrass plants, dry weight and leaf area were measured at 4, 8, 12, 16, 20, 24, 28, and 32 days after emergence. Five random plants of each species were collected each sampling time. With this data, RGR curves for both species grown with ideal conditions were developed.

In a second study, five plants of each species from each soil water potential treatment were harvested at 21, 24, 27, and 30 days after emergence. The experimental design was a split plot in a randomized complete block with three replications. Water stress treatment was the main plot, and sampling time was the sub-plot. Leaf area was measured with a portable leaf area meter (Licor, model LI-

3000, Lincoln, Nebraska). Leaves and shoots were oven dried at 65 C for 24 h and dry weight was determined.

The differences in MGR and MLAER were tested using an analysis of variance (ANOVA) procedure of SAS with ln-transformed differences in leaf area and dry plant weight as dependent variables as described by Cain and Ormrod (1984) and Poorter and Lewis (1986).

RGR, MGR, and MLAER were calculated using only the weight of aerial plant parts, leaf area data and the following equations:

$$RGR = (1/W)*(\ln W_2 - \ln W_1/t_2 - t_1);$$

$$MGR = (\ln W_2 - \ln W_1)/(t_2 - t_1);$$

$$MLAER = (\ln A_2 - \ln A_1)/(t_2 - t_1);$$

where:

A_1 = initial leaf area

A_2 = final leaf area

t_1 = initial time

t_2 = final time

W_1 = initial plant weight

W_2 = final plant weight

Plant Water Status Measurements

The youngest fully expanded leaves of different water stress treatments were used to measure total leaf water potential, stomatal conductance, and osmotic potential of both species. Measurements of leaf water potential were made with Scholander-type pressure chamber (Scholander et al., 1965). Leaves from different water stress treatments were excised from plants, wrapped in plastic bags, and immediately placed in the cylinder of the pressure chamber. The cylinder was previously filled with wet filter paper to avoid excessive transpiration during measurements.

Stomatal conductance was measured with a steady state porometer (Licor, model LI-1600, Lincoln, Nebraska) equipped with a narrowleaf aperture cap (1 cm^2 total exposure area), with concurrent measurements of irradiance and temperature (Campbell, 1975). Measurements were made on the adaxial leaf surface of both species.

Osmotic potentials were measured with a Wescor C52 chamber (Wescor Inc, Logan, Utah) coupled to a Wescor HR 33T microvoltmeter operated in the dewpoint mode. The last fully expanded leaves were excised and placed in a plastic bag. Leaves were then frozen and measured for osmotic potential within 7 days of freezing. Frozen leaf samples were allowed to thaw, plant sap was squeezed from each

leaf and collected on a filter paper disc until the disc was saturated. Discs were inserted into the sample chamber and the chamber allowed to equilibrate for two minutes. Voltage was adjusted to zero following chamber/leaf equilibration. Samples were cooled for 30 seconds and voltage was read 10 seconds after cooling ceased. A standard curve of osmotic potentials for 0.1, 0.2, 0.4, 0.6, and 1.0 molar solutions of KCl was developed for comparison.

Five plants of each water stress treatment were used to determine plant water status, and all the experiments were repeated.

Photosynthetic Rate Determination

Carbon exchange rate (CER) and transpiration were measured using a portable open-flow infrared gas analysis system, including an LCA-2 infrared CO_2 analyzer, ASUM mass flowmeter, and Parkinson broad-leaf chamber (Analytical Development Co.). Air was drawn from 1 m above the roof of the greenhouse; ambient CO_2 and humidity levels were used in all measurements. Humidity of the incoming airstream was measured in the empty chamber before each measurement on the leaf.

The chamber light sensor was recalibrated against a quantum sensor (LI-190 SB, Lambda Instruments Co. Inc.) placed inside the chamber, thus the values reported are based on light reaching the leaf inside the chamber. For the leaf temperature measurement, a thermocouple (0.13 mm wire) was used. Data were recorded using a computer-controller (Micromint, Inc. BCC-52) and an analog-digital board (Micromint, Inc. BCC-30) with a computer (Tandy Model 100) used for real-time display of environmental parameters, photosynthetic rate, leaf conductance, and other calculated values (Jurik et al., 1990).

Carbon exchange rate was calculated from the mass flow rate and the difference in CO_2 content of the air stream before and after leaf contact. Corrections for temperature and water vapor effects on the mass flow rate and for analyzer sensitivity to water vapor were made (Long and Hallgren, 1985; Jurik et al., 1990).

Stomatal conductance and intercellular CO_2 mole fraction were calculated according to Caemmerer and Farquhar (1981). Sorghum and woolly cupgrass plants have approximately an equal number of stomata on both surfaces of the leaf blade; conductance values were based on transpiration from the entire leaf but expressed per unit projected (one-side) leaf area.

The leaf chamber was held at the same position inside the growth chamber with a special stand during all the measurements. Plants were randomly selected from the water stress treatments, and all measurements were taken from the last fully expanded leaf. Measurements on a leaf were typically completed in 3 min after placing the chamber on a leaf. Sets of measurements for all treatments were made at 90 min intervals on plants of all the water stress treatments. Experiments were repeated.

Epicuticular Wax Determination

The youngest fully expanded leaf of shattercane and woolly cupgrass plants was selected after 9 days of water stress treatment, excised, leaf area determined, and the epicuticular wax removed with chloroform and quantified using a colorimetric method developed by Ebercon et al. (1977).

Standard curves for the quantity of epicuticular wax and absorbance were developed for both species. A standard solution was made by dissolving a known weight of epicuticular wax in chloroform. A range of concentrations were tested; absorbance was determined and a regression analysis describing the relationship of epicuticular wax quantity and absorbance at 590 nm was performed.

The standard curves were linear throughout the range of concentrations used (0, 100, 250, 500, and 1000 μg of bulk epicuticular wax per test tube). The regression equation for shattercane epicuticular wax was:

$$y = 0 + 0.000323\ X$$

and for woolly cupgrass epicuticular wax was:

$$y = 0 + 0.000354\ X,$$

where y = absorbance at 590 nm and x = amount of wax in μg. Leaves were immersed in chloroform for 30 seconds. The solution was filtered through a fritted disk (4.0-4.5 μm pore size) under suction. The filtrate was placed in a water bath at 85 C until all the chloroform was evaporated. An aliquot of 5 ml of acidic potassium bichromate ($K_2Cr_2O_7$) reagent was added, loosely capped with aluminum foil and placed in a water bath at 100 C for 30 minutes. After cooling, 12 ml of deionized water was added to the sample. Absorbance was determined with a spectrophotometer at 590 nm. The calculated amount of wax was divided by the corresponding leaf area and the resultant values expressed as μg cm^{-2}.

Epicuticular wax determination was made on 5 plants from each treatment on the last day of water stress. The experiment was repeated, and the results were analyzed by the ANOVA procedure of SAS.

ABA and IAA Determination

The last fully expanded shattercane and woolly cupgrass leaves from water stress treatments were excised, weighed, wrapped in aluminum foil, immediately frozen in liquid nitrogen, and stored in a freezer at -30 C until plant hormone determination.

Extraction and purification of ABA and IAA were made with the method described by Li (1989) which is summarized in the Figure 7. ABA and IAA extraction was made by grinding the leaf tissue 3 times with 80:20 (v/v) of acetone/water in a pre-chilled mortar and pestle in presence of the antioxidant 2,6-di-tert-butyl-4-methyl phenol (butylated hydroxy toluene, BHT). A known amount of trideuterated ABA (^{2}H-ABA) and ^{13}C labeled IAA ($^{13}C_6$-IAA), as internal standards, were added at the beginning of the extraction procedure. The extract was reduced to the aqueous phase before solvent partitioning.

ABA partitioning utilizes the weak acid characteristic of ABA (pKa = 4.8). This characteristic results in the ABA distribution between water and several solvents being pH-dependent. At pH of 8, ABA is almost completely dissociated; after mixing the aqueous ABA solution with hexane, all the ABA partitions to the aqueous phase. At pH of 2.5, ABA is almost completely undissociated, and with

Figure 7. Flow diagram of the extraction, separation, purification, and quantification of ABA and IAA, using ^{2}H-ABA and $^{13}C_6$-IAA as internal standards (Li, 1989)

2.5 g of leaves + ^{2}H-ABA and $^{13}C_6$-IAA (internal standards)

80% acetone (3X)

Extraction

Discard residual

Reduce to aqueous (pH 8.0)

Partition w/hexane (3X)

Discard hexane phase

Aqueous phase (pH 2.5)

Partition w/ethyl acetate

Discard aqueous phase

Ethyl acetate phase

↓

Dry

↓

70% MeOH (pH 8.0)

C-18 Sep-Pak

Discard

Elute

↓

Dry

↓

20% MeOH

HPLC C-18 reverse phase column
(20 - 100% MeOH gradient)

Discard

ABA and IAA fraction

↓

Dry

↓

Methylation (diazomethane)

↓

Dry (N_2)

↓

Elute in 200 µl 100% MeOH

↓

Dry (N_2) until 10 µl

↓

GC - MS

ethyl acetate, ABA is partitioned to the non-polar phase (Neill and Horgan, 1985).

ABA purification was accomplished with the use of C_{18} Sep-Pak cartridge (Water Associates, Watertown, MA), and HPLC reverse phase column with 5 μm particle size. UV detector (Beckman model 153) at 254 nm was used and the retention times for IAA and ABA were 1400 to 1600 and 1650 to 1850 seconds respectively. Finally, ABA and IAA were converted to the methyl ester (MeABA and MeIAA) with diazomethane.

ABA quantification was done using gas chromatography linked with mass spectrometry (GC-MS) (Hewlett Packard model 5890 and 5970, respectively), that relies on identification through the retention time and mass spectrum characteristics of the molecule. Selected ion monitoring (SIM) was used to detect the abundance of 162 and 190 atomic mass units (AMU) for ^{1}H-MeABA, 165 and 193 AMU for ^{2}H-MeABA; 130 and 189 AMU for MeIAA, and 136 and 195 AMU for $^{13}C_6$-IAA. The amount of ABA and IAA was calculated by isotope dilution equations (Magnus et al., 1980).

Two shattercane plants from each water stress treatment were sampled and analyzed for ABA at 2, 3, 4, and 5 days after the initiation of water stress treatment (Experiment 1). Two shattercane plants of each water stress treatment

were analyzed for ABA and IAA at 1, 3, 5, and 7 days after the initiation of water stress treatments (Experiment 2). Two woolly cupgrass plants from each water stress treatment were sampled and analyzed for ABA and IAA at 2, 4 and 6 days after the initiation of water stress treatment (Experiment 3). Regression analysis was conducted with each set of water stress treatments.

Results and Discussion

Leaf Surface Description

The SEM photographs of shattercane leaf surfaces at different magnifications demonstrate a common pattern toward more epicuticular wax deposition under more intense water stressed conditions (Figures 8, 9 and 10, plates A, B, C, and D). The same trend was not clear in woolly cupgrass leaves, but differences in epicuticular wax architecture are noticeable (Figure 10, plates I, G, and H). Figure 11 shows an overall view of both leaf surfaces (plates A, and B). Both grasses demonstrate classical patterns of leaf anatomy for grasses such as bicellular microhairs (Figure 8, plate B) and elevated intercostal areas with stomata aligned in one or two files (Figure 11, plates A and B). A transversal cut of a shattercane cuticle, with a detail of epicuticular wax architecture is shown in Figure 11, plate C.

Figure 8. Leaf surface morphology of shattercane (A, B, C, and D) and woolly cupgrass (E, F, G and H) as observed with scanning electron microscope (SEM). A and E = -0.03 MPa, B and F = -0.4 MPa, C and G = -0.8 MPa, and D and H = -1.2 MPa. Scale marker = 50 μm

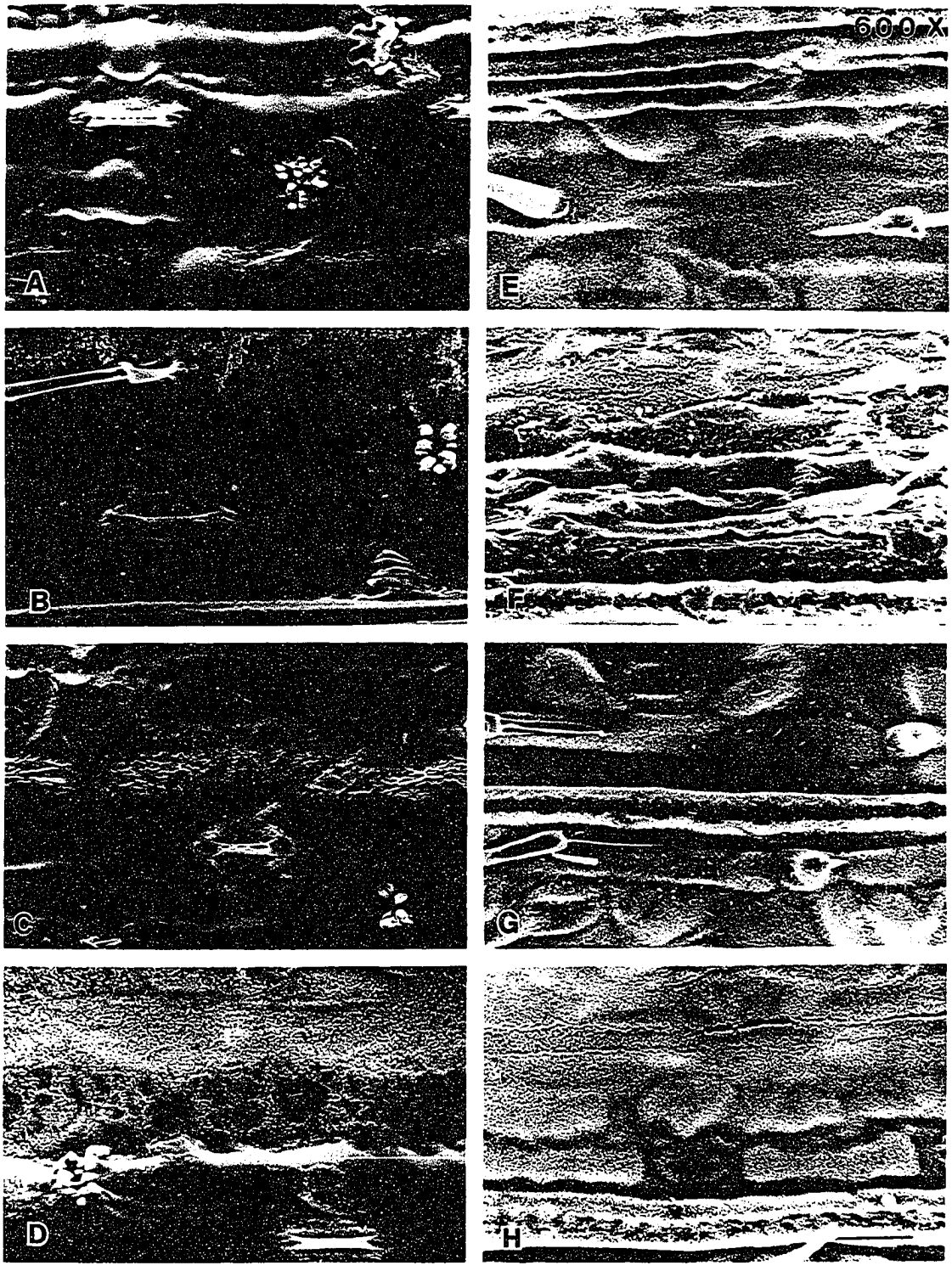

A
B
C
D
E
600X
F
G
H

Figure 9. Leaf surface morphology of shattercane (A, B, C, and D) and woolly cupgrass (E, F, G and H) as observed with scanning electron microscope (SEM). A and E = -0.03 MPa, B and F = -0.4 MPa, C and G = -0.8 MPa, and D and H = -1.2 MPa. Scale marker = 5 μm

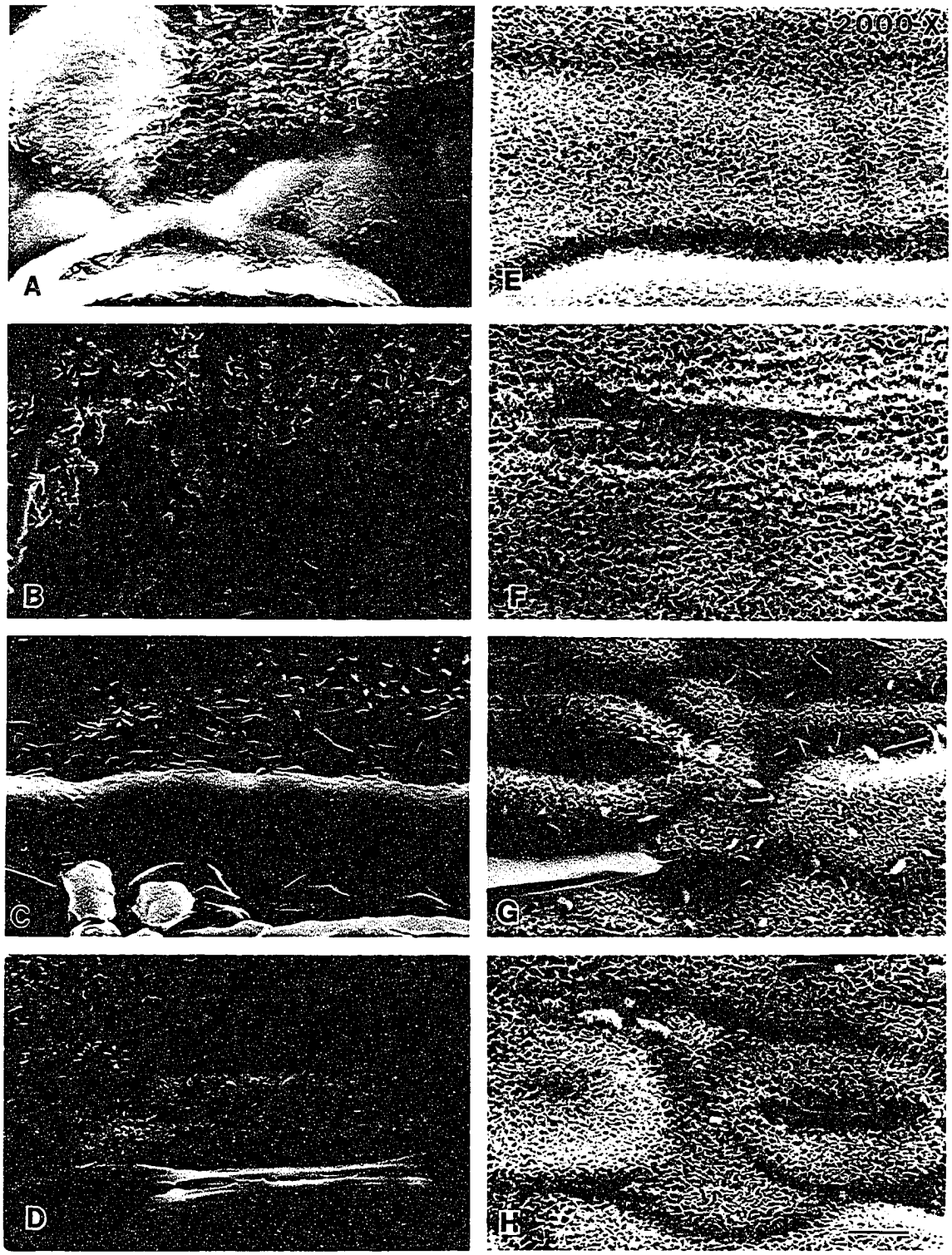

A
B
C
D
E
2000 X
F
G
H

Figure 10. Leaf surface morphology of shattercane (A, B, C, and D) and woolly cupgrass (E, F, G and H) as observed with scanning electron microscope (SEM). A and E = -0.03 MPa, B and F = -0.4 MPa, C and G = -0.8 MPa, and D and H = -1.2 MPa. Scale marker = 10 μm

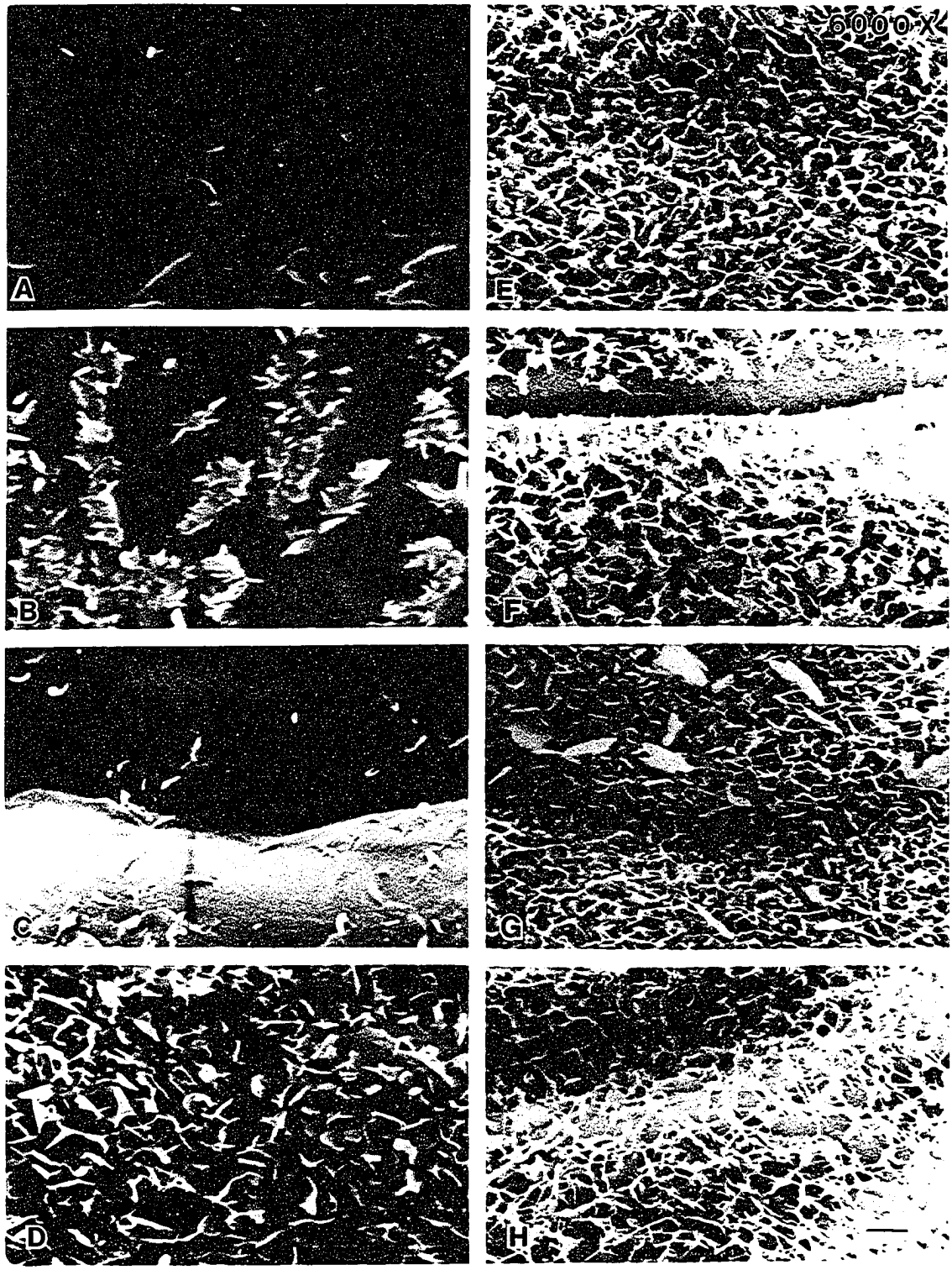

A
B
C
D
E
6000 X
F
G
H

Figure 11. Overall view of leaf surface morphology of A. shattercane and B. woolly cupgrass as observed with scanning electron microscope (SEM). Scale marker = 50 μm.
C. Cross-sectional view of [Sorghum bicolor (L.) Moench] cuticle showing epicuticular wax architecture. Scale marker = 5 μm

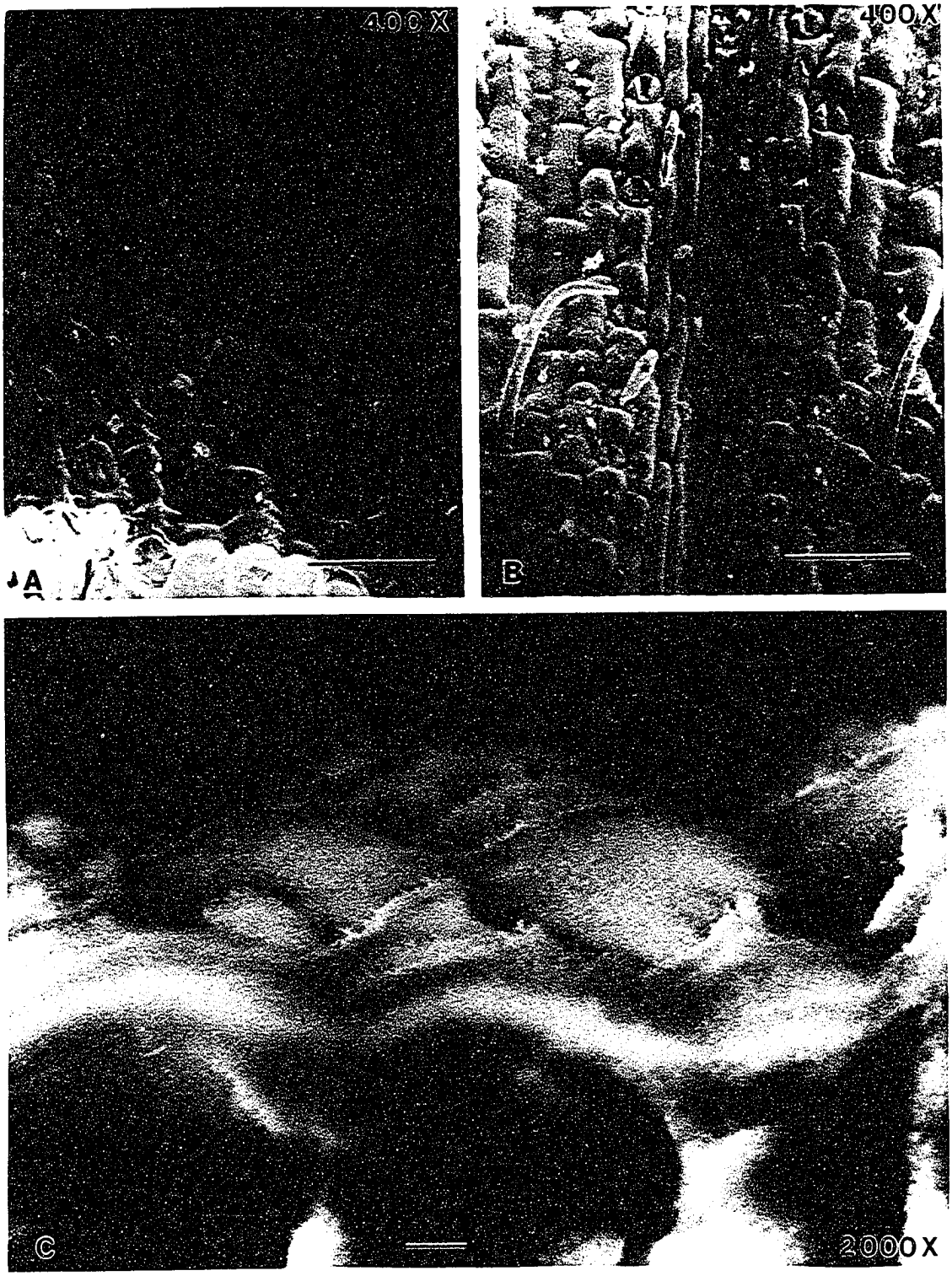

400 X
A
400 X
B
C
2000 X

Figure 12. Cryo-SEM leaf fractures of shattercane (A, B, C, and D) and woolly cupgrass (E, F, G, and H). A and E = -0.03 MPa, B and F = -0.4 MPa, C and G = -0.8 MPa, and D and H = -1.2 MPa. Scale marker = 50 μm

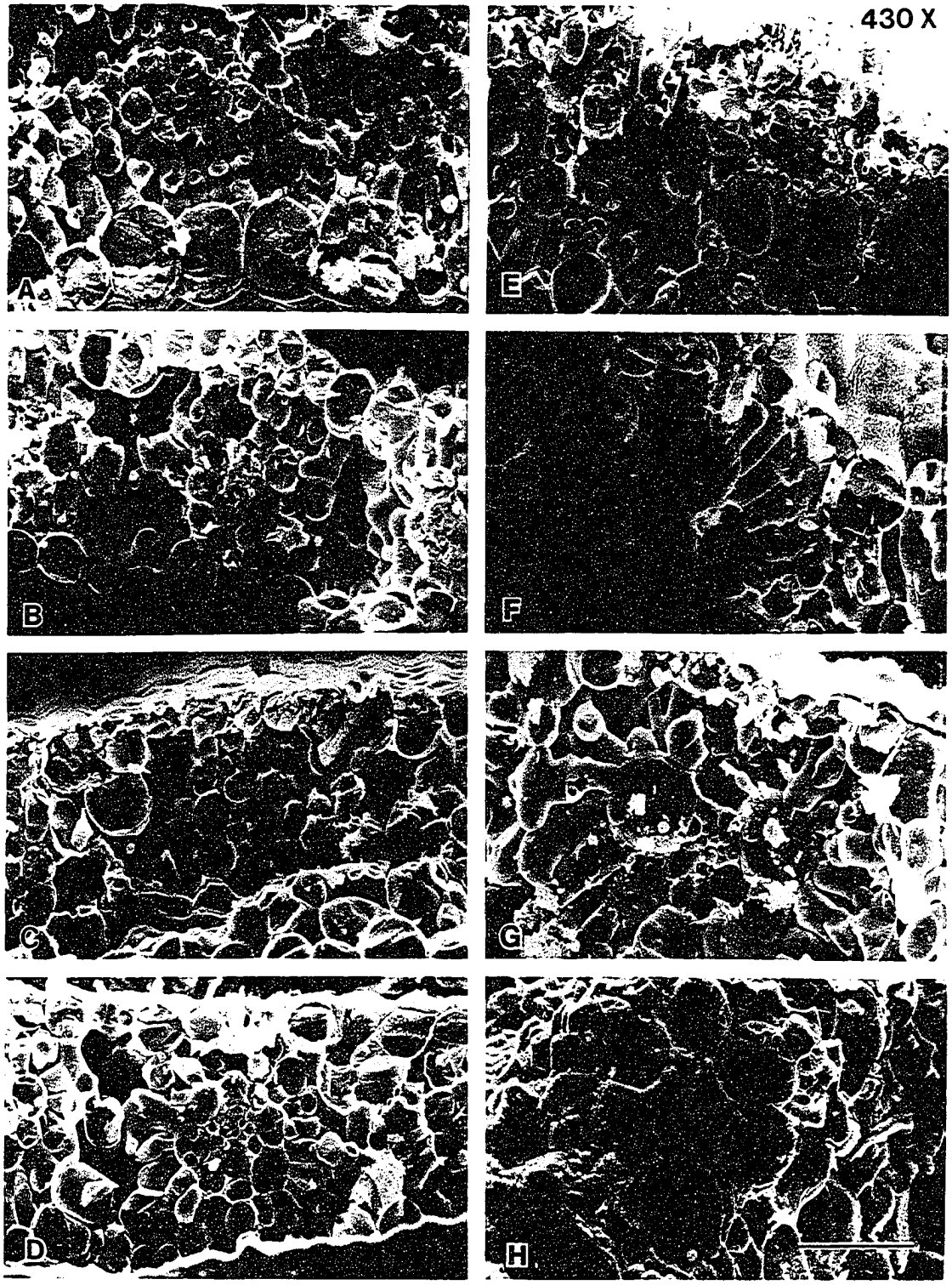

430 X
A
B
C
D
E
F
G
H

Figure 12 shows cryo-SEM fractures of both species under different degrees of water stress. Leaves of shattercane and woolly cupgrass growing under well-watered conditions demonstrated more intercellular spaces than plants growing under water stress conditions.

Growth Characterization

Growth measurements were used to integrate the responses of metabolic and physiological processes to water

Table 3. Dry weight (DW) and leaf area (LA) of shattercane and woolly cupgrass growing without water stress

Days after emergence (DAE)	Shattercane DW[a]	Shattercane LA[b]	Woolly cupgrass DW	Woolly cupgrass LA
4	0.14	32	0.12	25
8	0.28	53	0.21	48
12	0.58	85	0.43	94
16	0.90	151	0.87	164
20	1.35	225	1.29	229
24	1.93	301	2.50	303
28	2.64	382	3.92	392
32	3.58	473	4.98	491

[a]Dry weights are expressed in g/plant, each value is the average of five plants.

[b]Leaf area are expressed in cm^2/plant, each value is the average of five plants.

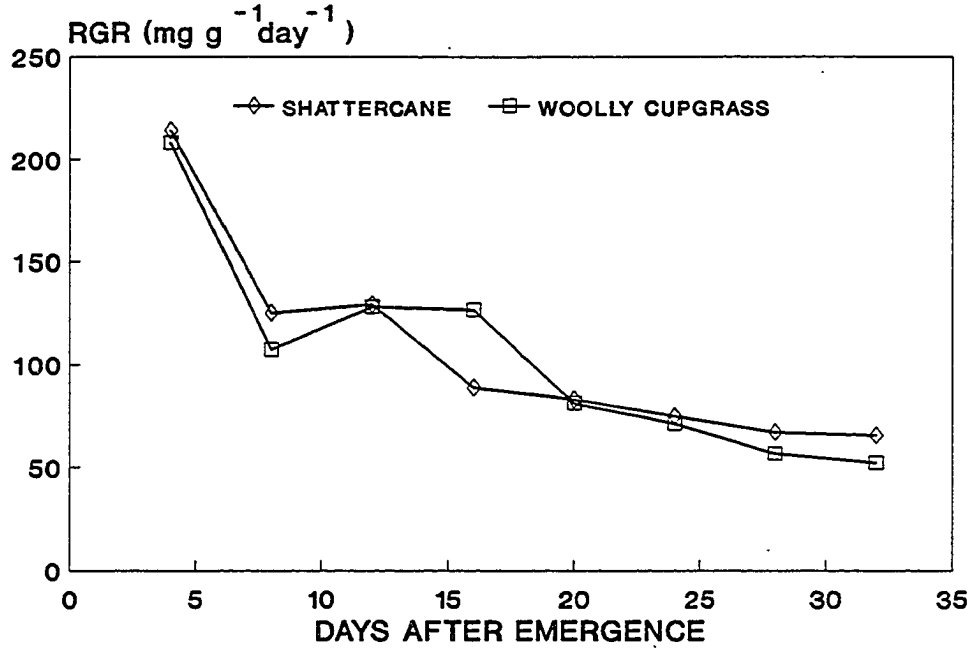


Figure 13. Relative growth rate (RGR) (mg g^{-1} day^{-1}) of shattercane and woolly cupgrass growing under well-watered conditions. Harvest intervals were 4 days. Each value is the average of 5 plants

stress. The results of an initial study, describing well-watered shattercane and woolly cupgrass plants dry weight and leaf area characteristics are shown in Table 3. Table 1 in the Appendix shows the means and standard deviation values for this experiment. Results confirm that all the studies were conducted during the exponential growth period for both weeds.

The progression of the derived parameters RGR, MGR, and MLAER for the same experiment are shown in Figures 13, 14, and 15 respectively.

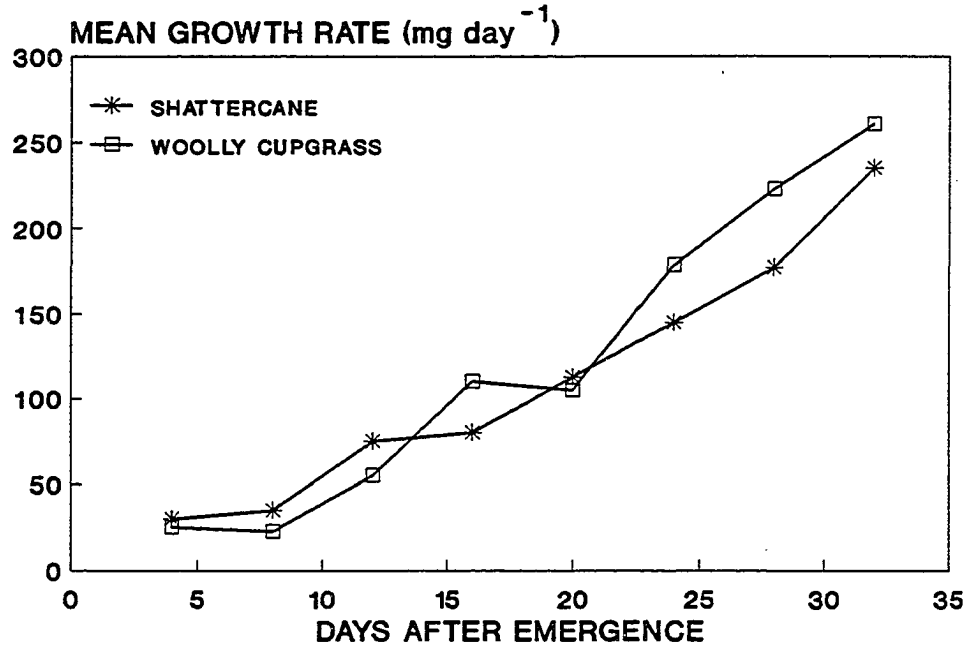


Figure 14. Mean growth rate (MGR) (mg day^{-1}) of shattercane and woolly cupgrass growing under well-watered conditions. Harvest intervals were 4 days. Each value is the average of 5 plants

ANOVA analysis of ln-transformed growth data revealed a significant effect of intensity of water stress on MLAER and MGR in both species. For shattercane, MGR decreased with increasing water stress treatment; plants subjected to -0.4 MPa demonstrated 30% reduced growth rate as compared with well-watered plants (Figure 16, and Table 2 in the Appendix); however, the plants did increase weight during the period of observation. The mean growth rate was negative in the -0.8 and -1.2 MPa treatments due to leaf senescence.

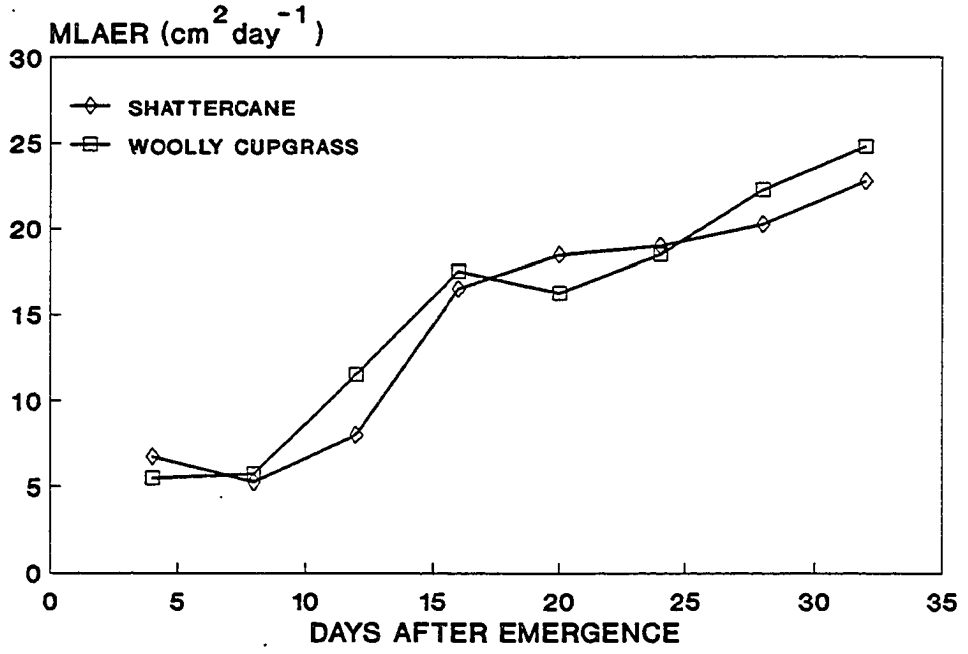


Figure 15. Mean leaf area expansion rate (MLAER) (cm^2 day^{-1}) of shattercane and woolly cupgrass growing under well-watered conditions. Harvest intervals were 4 days. Each value is the average of 5 plants

The senescence pattern showed that older leaves died first.

For woolly cupgrass, MGR demonstrated a significant interaction between soil water potential treatment and time of sampling (Figure 17, and Table 3 in the Appendix). Differences in the growth of plants under water stress treatments and the well-watered plants increased with time after water stress initiation. Plants subjected to -0.4 and -0.8 MPa reduced growth by 29% and 11% of the well-

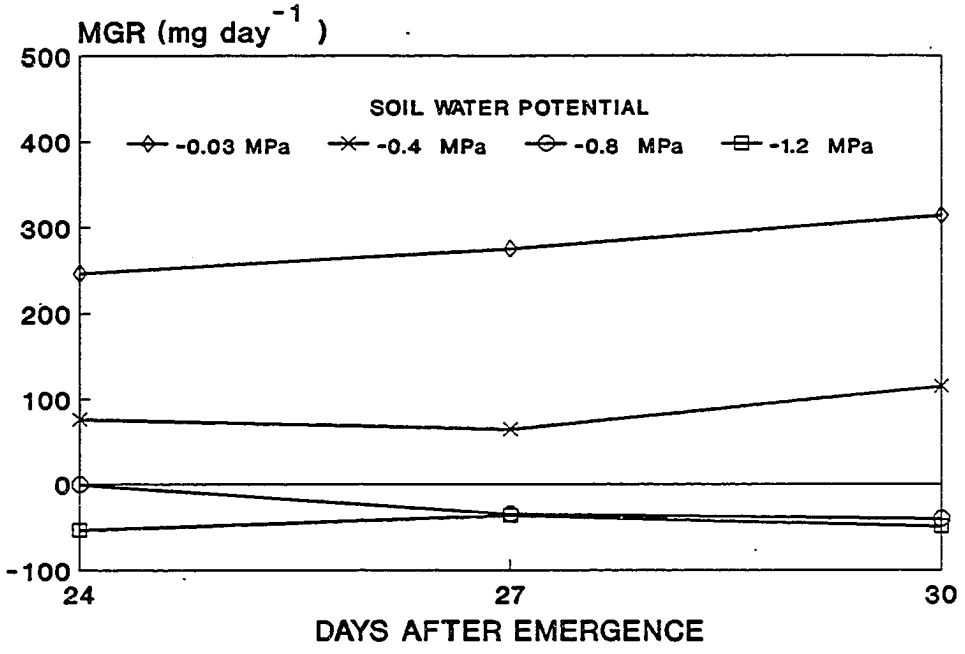


Figure 16. Mean growth rate (MGR) (mg day^{-1}) of shattercane plants at different levels of soil water potential. Harvest intervals were 3 days. Each value is the average of 5 plants

watered plants, respectively. The MGR was negative for the-1.2 MPa treatments. The senescence pattern in woolly cupgrass demonstrated that the last tiller generation died first.

Shattercane and woolly cupgrass leaf expansion were significantly affected by water stress; mean leaf area expansion rate was very sensitive to all the stress treatments (Figure 18 and 19, and Tables 4 and 5 in the Appendix). These results agree with reports that describe

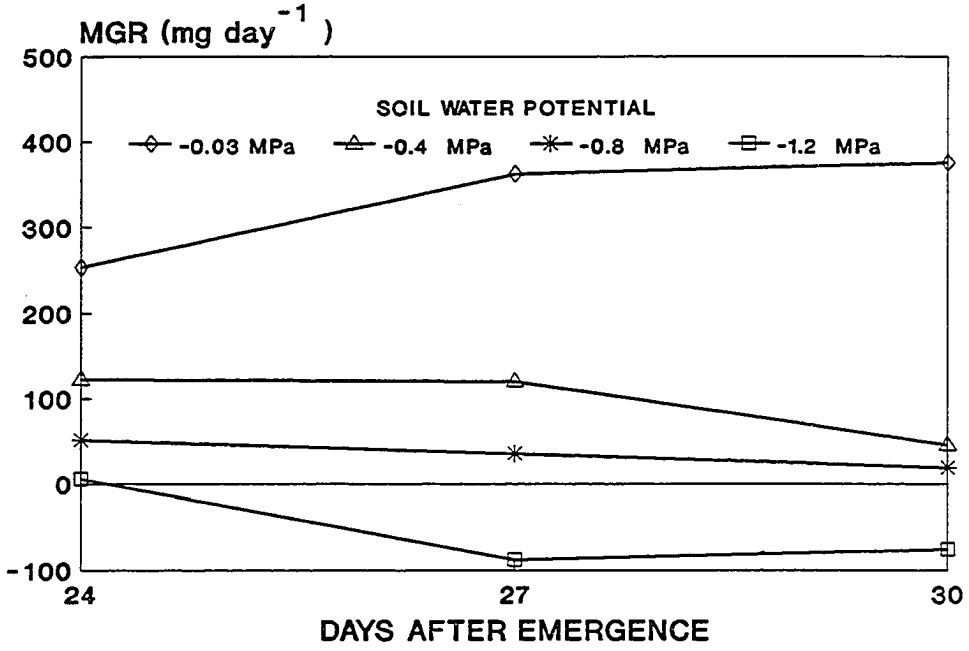


Figure 17. Mean growth rate (MGR) (mg day^{-1}) of woolly cupgrass plants at different levels of soil water potential. Harvest intervals were 3 days. Each value is the average of 5 plants

leaf expansion as a physiological process very sensitive to water stress (Boyer, 1970; Hsiao, 1973). In both species, leaf rolling was an early morphological expression of water stress conditions whereas leaf senescence was observed later under more severe water stress.

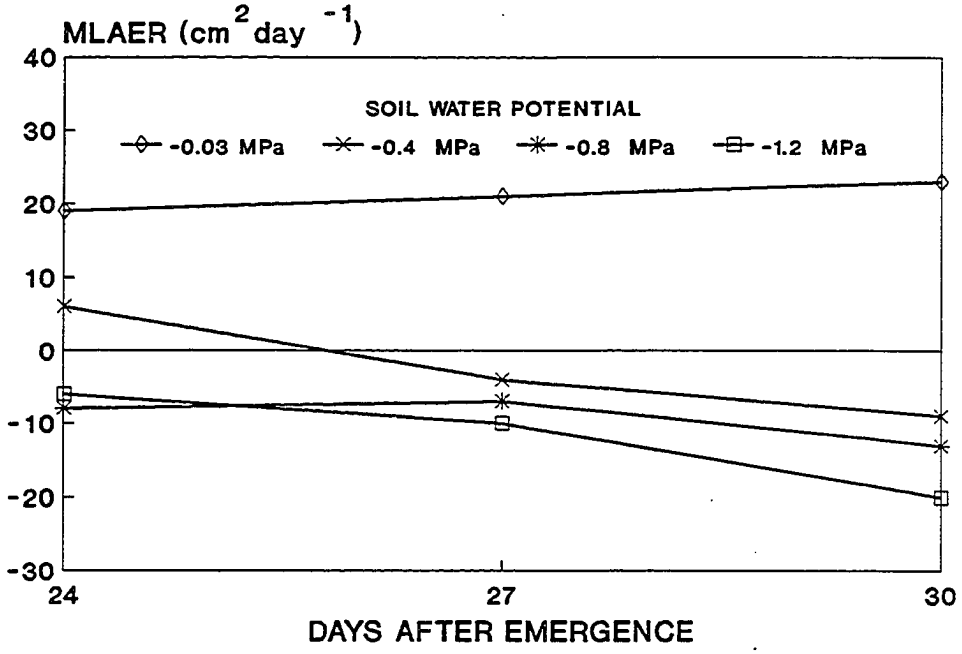


Figure 18. Mean leaf area expansion rate (MLAER) (cm^2 day^{-1}) of shattercane plants growing at different levels of soil water potential. Harvest intervals were 3 days. Each value is the average of 5 plants

All the above results are supported in the literature. Growth reduction under water stress conditions is a well documented phenomenon (Akey and Morrison, 1984; Hsiao and Acevedo, 1974; Westgate and Boyer, 1985). Morphological changes like leaf rolling (Bittman and Simpson, 1989) and leaf senescence (Aparicio-Tejo and Boyer, 1983) were also reported.

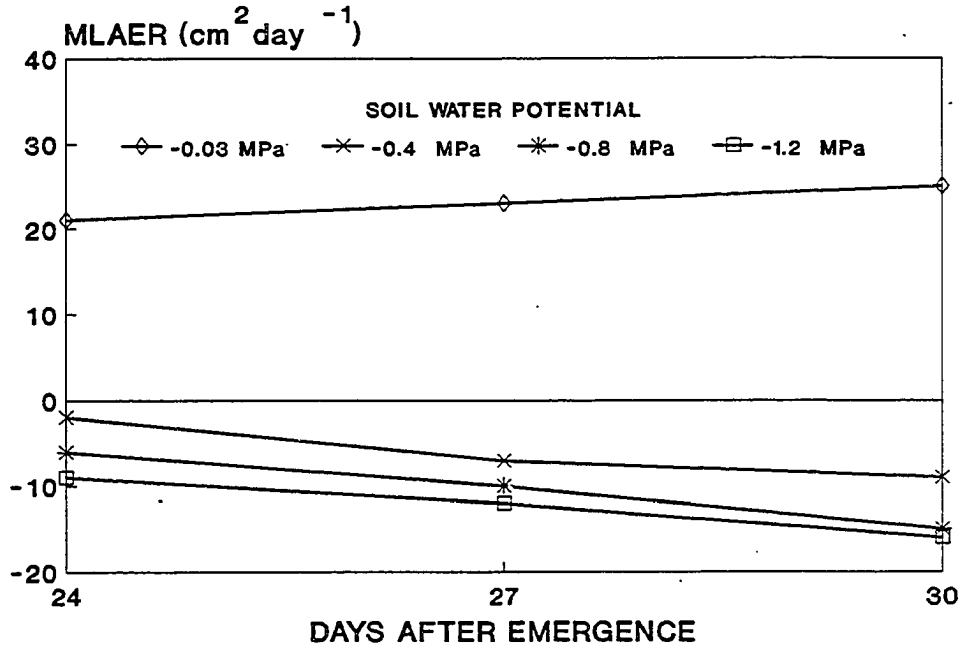


Figure 19. Mean leaf area expansion rate (MLAER) (cm^2 day^{-1}) of woolly cupgrass plants growing at different levels of soil water potential. Harvest intervals were 3 days. Each value is the average of 5 plants

Plant Water Status Measurements

Leaf water potential exhibited a daily variation, but was highly correlated with soil water potential treatment in both species. Leaf water potential followed the temperature trend (that in turn drives the water saturation deficit).

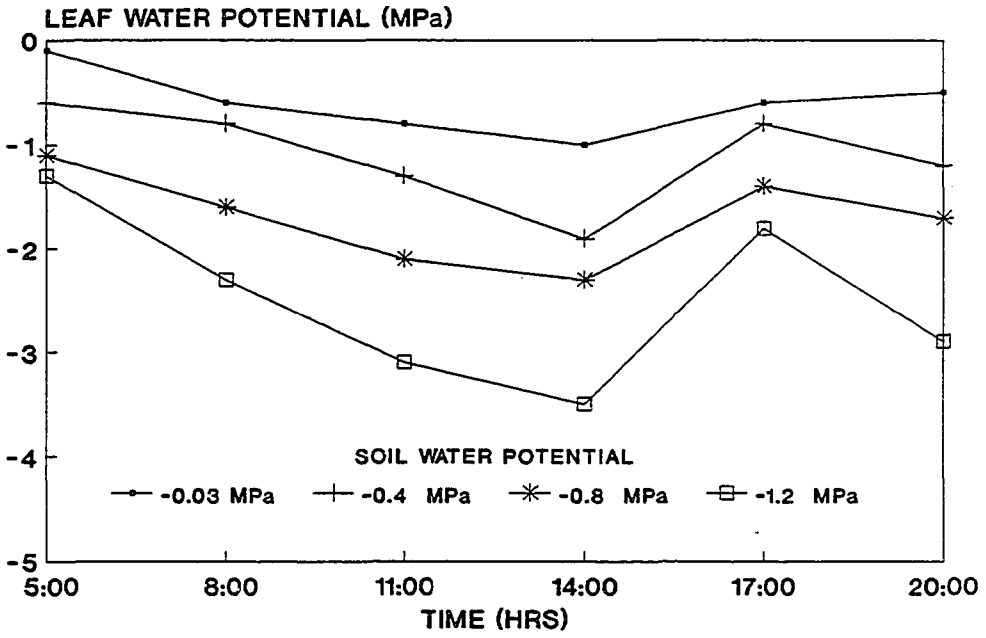


Figure 20. Changes in leaf water potential of shattercane plants subjected to different treatments of soil water potential on day 8 of water stress. Each value is the average of 5 plants

Differences between soil water potential treatments for shattercane leaf water potential are clearly demonstrated in Figure 20. The leaf water potential recovery after 1400 hrs was due to the effect of irrigation.

Woolly cupgrass plants follow similar trends for leaf water potential and time (Figure 21). Leaf water potential means and standard deviations are displayed in Table 6 in the Appendix.

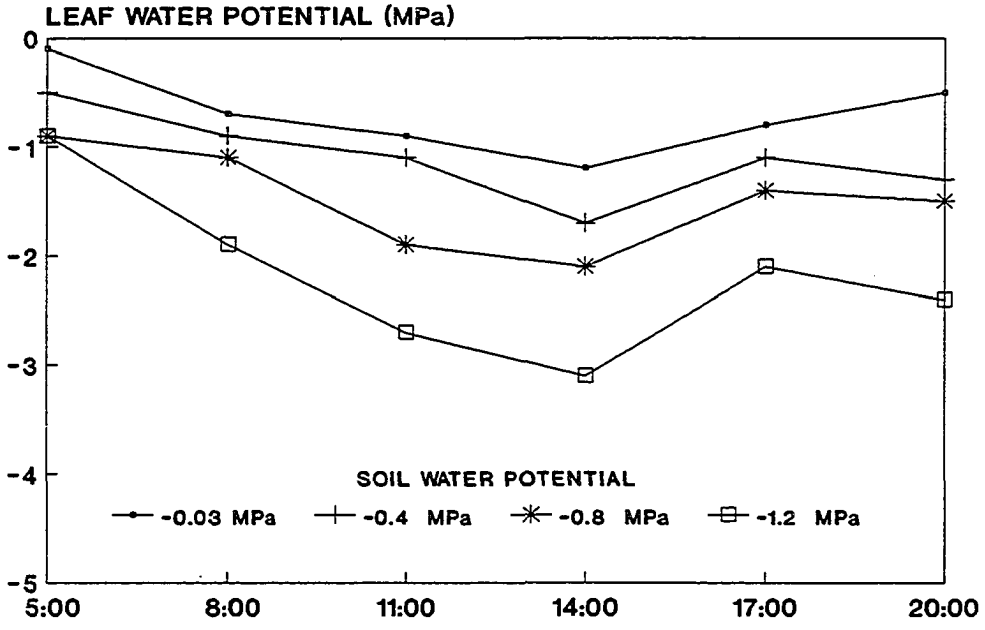


Figure 21. Changes in leaf water potential of woolly cupgrass plants subjected to different treatments of soil water potential on day 8 of water stress. Each value is the average of 5 plants

Stomatal conductance of shattercane and woolly cupgrass plants on day 8 after the initiation of water stress was variable for both species (Figure 22, 23, and Table 7 in the Appendix). In both species, an increase in leaf conductance corresponding to the beginning of light period was observed. A measurement made on all treatments during the dark period of day 8 demonstrated negligible stomatal conductance. Sustained nocturnal stomatal closure

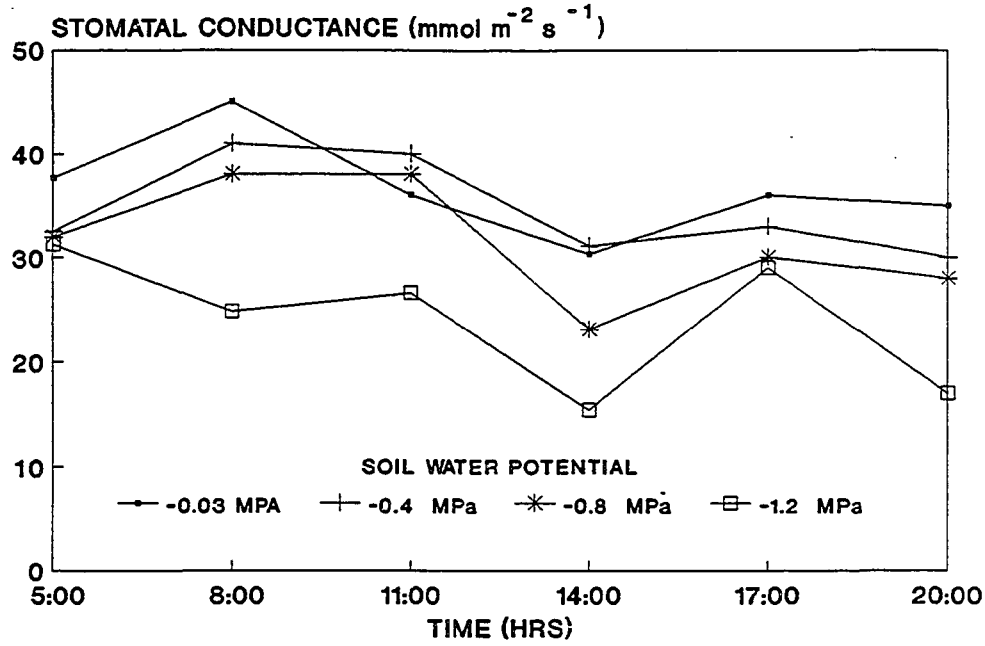


Figure 22. Changes in stomatal conductance of shattercane plants subjected to different treatments of soil water potential on day 8 of water stress. Each value is the average of 5 plants

appears to be a feature of grasses (Muchow et al., 1980). No significant differences between water stress treatments were found in shattercane stomatal conductance at 0500 hrs; at 0800 and 1100 hrs only plants in the -1.2 MPa treatment showed a significantly reduced stomatal conductance. At 1400, no differences in stomatal conductance were found between plants subjected to -0.03 and -0.4 MPa.

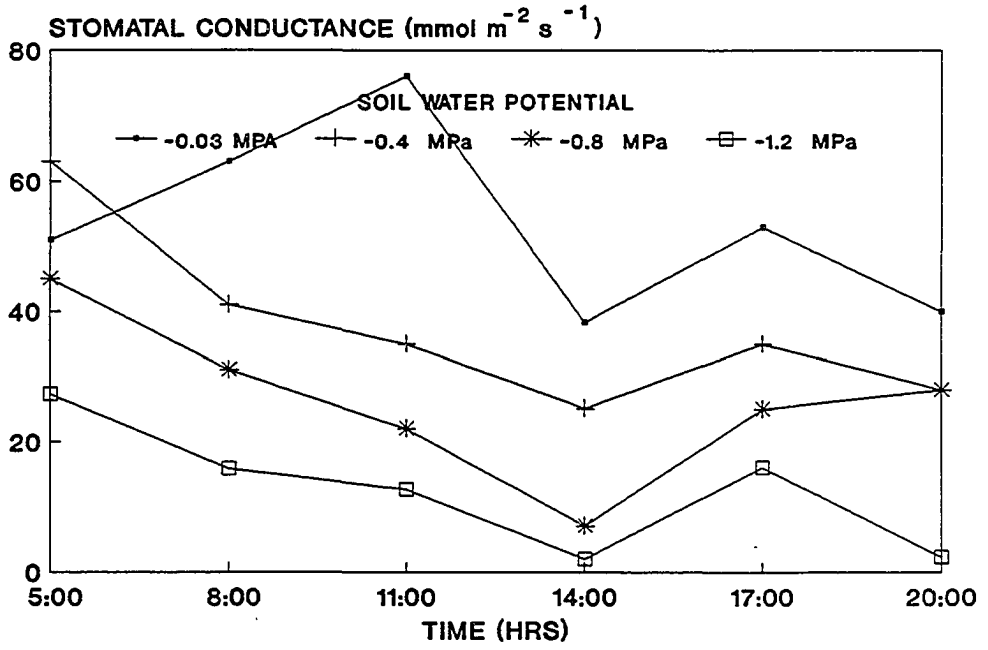


Figure 23. Changes in stomatal conductance of woolly cupgrass plants subjected to different treatments of soil water potential, in the day 8 of water stress. Each value is the average of 5 plants

At 1700 hrs, no differences between treatments were found in stomatal conductance likely due to the irrigation effect. Results suggest that leaf water potentials of shattercane plants must be less than -1.5 MPa to reduce stomatal conductance.

Stomatal conductance was more sensitive to water stress treatments in woolly cupgrass than shattercane plants (Figure 23).

At 0800 and 1100 hrs, dramatic differences in stomatal conductance between well-watered plants and stressed plants were observed. Plants of the -0.4, -0.8 and -1.2 MPa treatments demonstrated a daily tendency to decrease stomatal conductance; this trend was only partially reverted by the afternoon irrigation (Figure 23).

Osmotic adjustment was not clear for the conditions of this experiment. The small volume of the pots used may cause an abrupt decline in plant water potential thus reducing the plant capacity for osmotic adjustment (Table 8 in the Appendix).

Photosynthetic Rate Determination

Ambient air CO_2 mole fraction varied from 0.000303 to 0.000349 during photosynthetic determinations; the prevailing atmospheric pressure in Ames, Iowa was 98.3 kPa. Carbon exchange rate (CER) of non-stressed shattercane and woolly cupgrass leaves increased with increasing PPFD. At constant PPFD, CER was constant or slightly increased between leaf temperatures of 23 to 31 C but declined at higher temperatures (35-36 C). Photosynthetic rate of both weeds was highly correlated with levels of water strdss (Figures 24 and 25, and Table 9 in the Appendix).

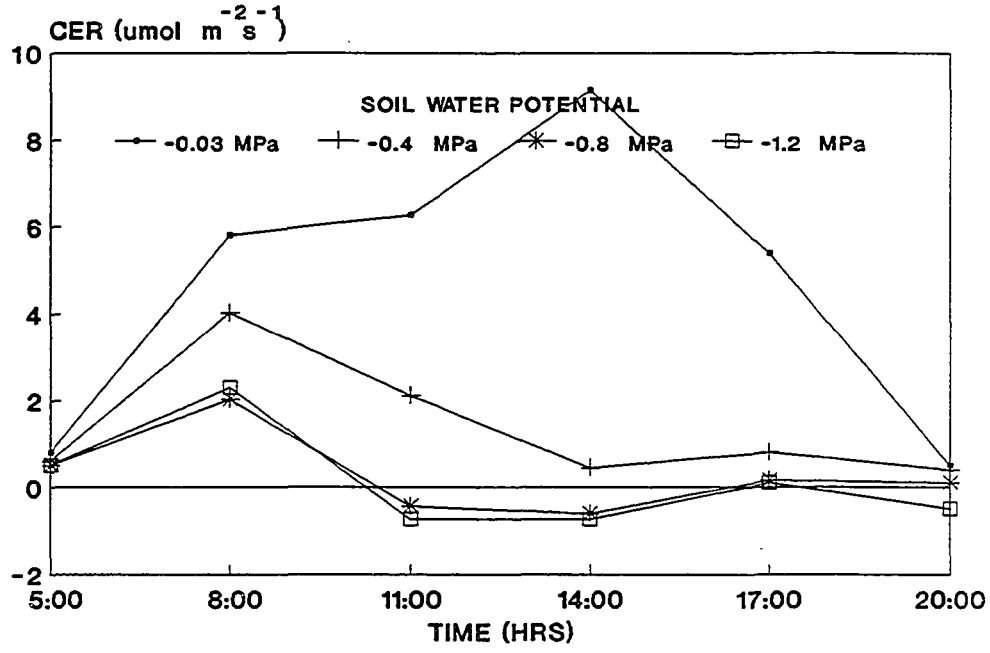


Figure 24. Daily time course of CER in shattercane plants grown at different levels of soil water potential on day 8 of water stress. Each value is the average of 5 plants

Photosynthesis decreased with decreasing leaf water potential. The decline in photosynthetic activity was partially related to decreased stomatal conductance in leaves of stressed plants.

Photosynthetic rate reductions due to increasing water stress have been observed in a variety of plant species. Stomatal closure was not evident in shattercane plants

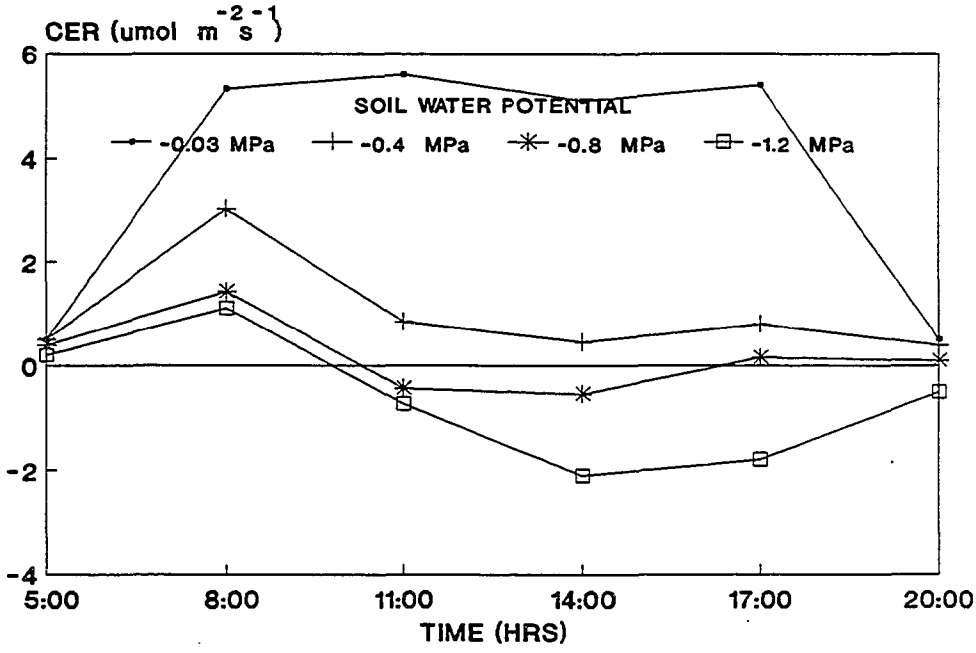


Figure 25. Daily time course of CER in woolly cupgrass plants grown at different levels of soil water potential on day 8 of water stress. Each value is the average of 5 plants

under medium water stress (-0.4 and -0.8 MPa), however photosynthesis was severely reduced. These results indicated that biochemical processes were affected. Deprivation of CO_2 limits the amount of $NADP^+$ available; under these circumstances, O_2 is an alternative electron

acceptor generating free radicals (superoxide and hydrogen peroxide) thus leading to the photodestruction of the photosynthetic apparatus (Rhodes, 1987).

Epicuticular Wax Determination

In shattercane, plants grown at soil water potential treatments of -0.4 and -0.8 MPa had more epicuticular wax than plants grown under well-watered conditions (8.75, 6.93 and 5.84 $\mu g\ cm^{-2}$, respectively). However, plants grown at -1.2 MPa of soil water potential contained less epicuticular wax than the well-watered plants (4.02 versus 5.84 $\mu g\ cm^{-2}$, respectively). The differences between treatments were significant at the 5% level (Table 10 in the Appendix). Shattercane plants growing at -1.2 MPa of soil water potential are strongly affected physiologically and morphologically; this may explain the reduced wax deposition.

In woolly cupgrass, plants grown at -0.4 MPa of soil water potential contained the maximum amount of epicuticular wax, followed by plants of the -0.03, -0.8 and -1.2 MPa (10.33, 6.94, 6.81 and 3.68 $\mu g\ cm^{-2}$, respectively).

Table 4. Epicuticular wax content of shattercane and woolly cupgrass plants growing under different soil water potential treatments[a]

	Soil water potential			
	-0.03MPa	-0.4MPa	-0.8MPa	-1.2MPa
Shattercane	8.75	6.93	4.02	5.84
Woolly cupgrass	10.33	6.81	3.69	6.94

[a]Expressed in $\mu g\ cm^{-2}$. Each value is the average of ten plants.

The differences between treatments were significant at the 5% level (Table 10 in the Appendix).

In general, these results agree with previous reports (Baker, 1974; Jordan, et al., 1983; Pitty, 1988; Skoss, 1955) indicating an increase in epicuticular wax with

increases in water stress. However, more wax was deposited under mild water stress than more severe stress conditions (Table 4).

ABA and IAA Determination

Well watered shattercane plants maintained a basal level of ABA during the period of observation, however, differences in ABA contents were clearly detected between experiments (a mean of 30 ng/g of fresh material in the experiment 1 as compared with a mean of 50 ng/g of fresh material in the experiment 2). Differences between experiments may be ascribed to the impossibility of maintaining exactly the same experimental conditions during the experiment.

ABA accumulation in plants under water stress was detected in both experiments; the accumulation was more noticeable in the first experiment (three to five fold compared to controls) (Figure 26). The ABA content in

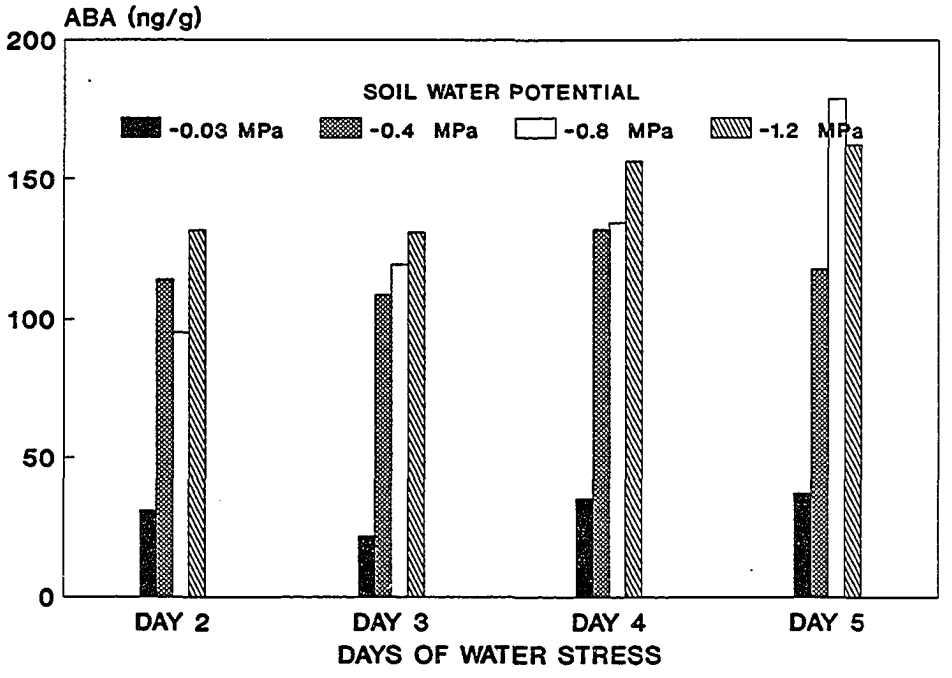


Figure 26. ABA accumulation in shattercane plants growing under different levels and durations of soil water potential. Each mean is the average of two samples. ABA is expressed in ng/g of fresh tissue. Data from experiment 1

plants growing under soil water potentials of -0.8 MPa and -1.2 MPa clearly increased during the stress period. Plants growing in -0.4 MPa of soil water potential contained more ABA than well-watered plants throughout the

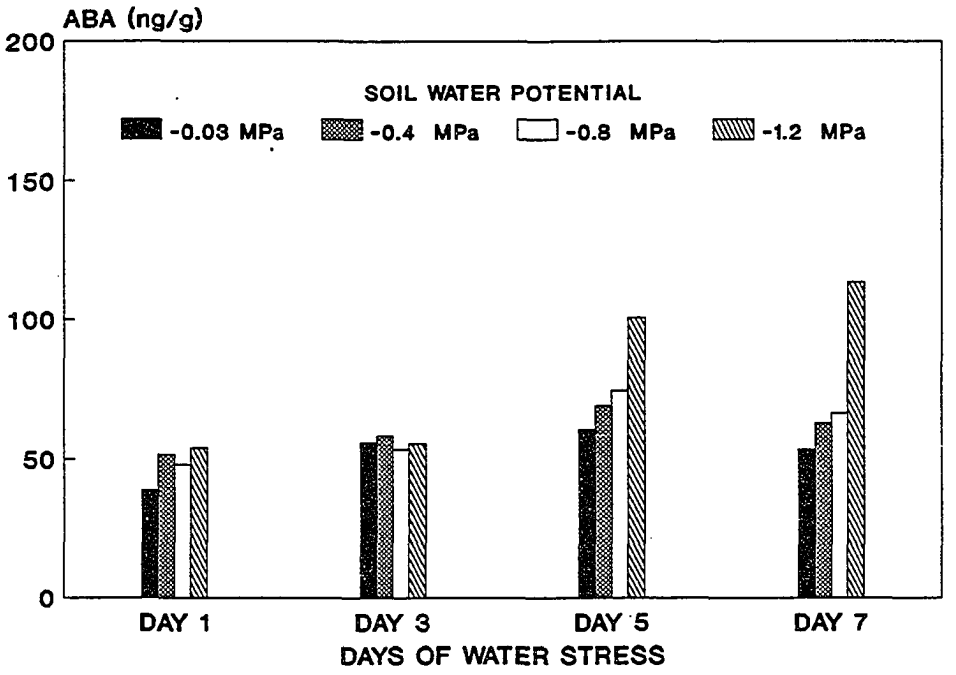


Figure 27. ABA accumulation in shattercane plants growing under different levels and durations of soil water potential. Each mean is the average of two samples. ABA is expressed in ng/g of fresh tissue. Data from experiment 2

study, but ABA levels remained constant during the study period (Figure 27). ABA data were pooled and analyzed together with regression techniques. Increases in ABA content were observed in all stress treatments, but especially so for the -1.2 MPa treatments (Table 5).

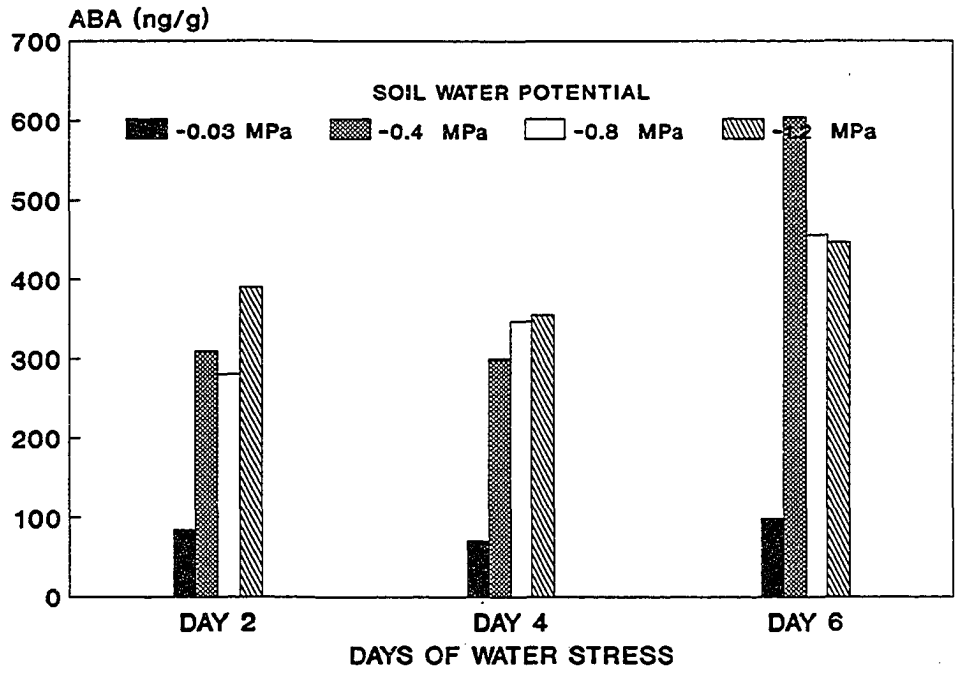


Figure 28. ABA accumulation in woolly cupgrass plants growing under different levels and durations of soil water potential. Each mean is the average of two samples. ABA is expressed in ng/g of fresh tissue. Data from experiment 3

In the experiment 3, woolly cupgrass plants growing under well-watered conditions demonstrated a steady (basal) content of ABA. All the stress treatments demonstrated a three to five fold increase in the ABA content.

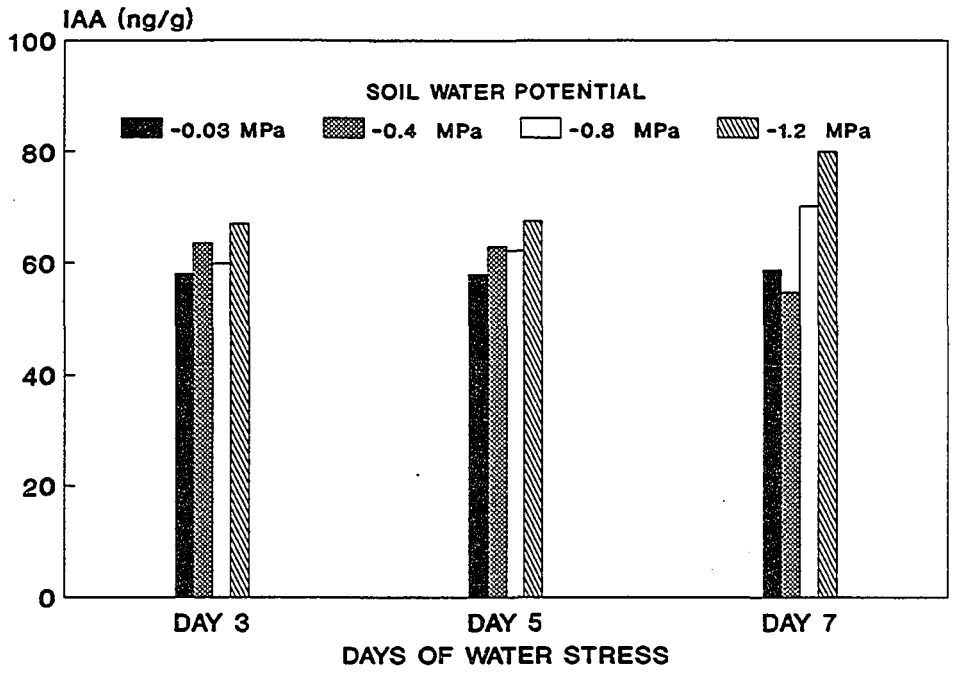


Figure 29. IAA content in shattercane plants growing under different levels and durations of soil water potential. Each mean is the average of two samples. IAA is expressed in ng/g of fresh tissue

The accumulation was more noticeable in the treatment of -0.4 MPa (Figure 28).

There were no differences in IAA content of shattercane plants growing at different levels of water stress. IAA content did not change with duration of stress treatment (Figure 29).

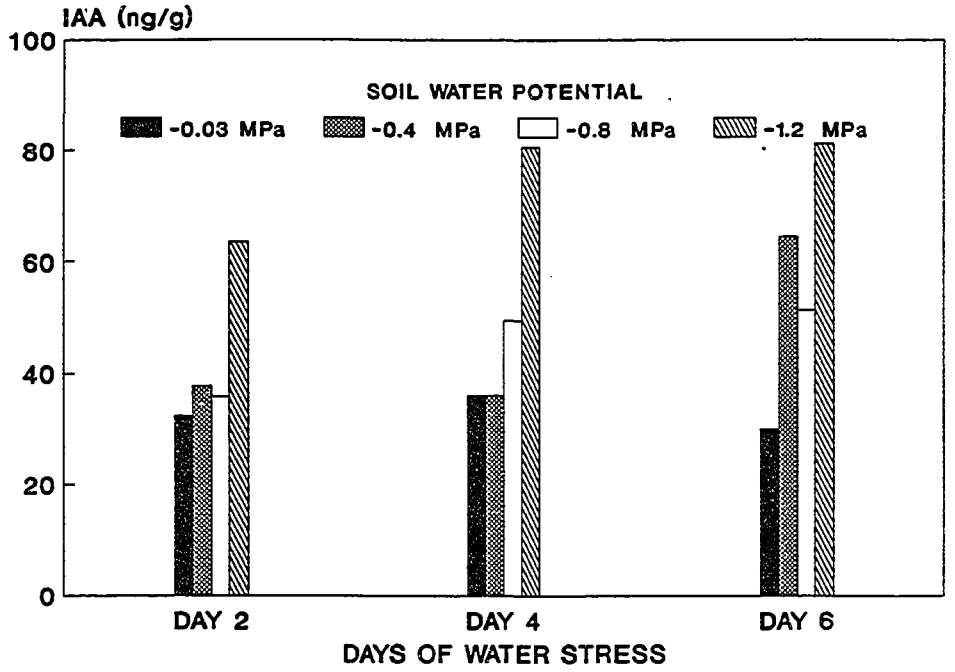


Figure 30. IAA content in woolly cupgrass plants growing under different levels and durations of soil water potential. Each mean is the average of two samples. IAA is expressed in ng/g of fresh tissue

The IAA content of woolly cupgrass was higher in plants under stress conditions. The accumulation was significant in the -1.2 MPa treatment after the second day of water stress. Maximum IAA accumulation was demonstrated during the sixth day of water stress for all the stress treatments (Figure 30).

Table 5. Statistical analysis of ABA content (in ng/g of fresh weight) on shattercane and woolly cupgrass plants between 1 and 7 days after initiation of water stress treatments[a]

Water stress treatments	a	b	n	Prob > t	R^2	CV
Shattercane[b]						
-0.03 MPa	31.5	3.9	16	0.18	0.39	25.76
-0.4 MPa	90.4	0.2	16	0.97	0.71	37.91
-0.8 MPa	78.4	3.9	16	0.63	0.66	39.15
-1.2 MPa	84.9	7.8	16	0.35	0.22	31.36
Woolly cupgrass[c]						
-0.03 MPa	40.2	1.1	4	0.58	0.45	17.86
-0.4 MPa	93.7	-0.5	4	0.75	0.23	21.11
-0.8 MPa	87.8	1.2	4	0.82	0.66	17.15
-1.2 MPa	95.4	6.3	4	0.83	0.78	27.91

[a]a (intercept), b (slope), n (sample size), R^2 (correlation coefficient), and CV (coefficient of variation in percent).

[b]Each sample represents 8 data per treatment averaging experiments 1 and 2.

[c]Each sample represent 4 data per treatment.

Conclusions

The results of these studies demonstrated several morphological and physiological changes produced in shattercane and woolly cupgrass plants grown under water stress. Both plants exhibited decreased dry matter accumulation and leaf area expansion due to water stress treatments. Initially, leaf rolling, followed by leaf senescence, were indicators of morphological adaptations to water stress. Data indicated that leaf area expansion was more sensitive to water stress than dry matter accumulation.

All of the parameters associated with plant water status were affected. Leaf water potential appeared to be the parameter most affected in both species. Stomatal conductance demonstrated a specific response. Shattercane stomata responded less under severe water stress conditions than woolly cupgrass plants. However, osmotic adjustment by shattercane and woolly cupgrass was not demonstrated in these experiments.

Photosynthesis was greatly reduced in shattercane and woolly cupgrass, suggesting the possibility that non-stomatal factors superimpose its action to stomatal control, resulting in a reduced CER.

Abscisic acid content of shattercane and woolly cupgrass leaves and IAA content of woolly cupgrass leaves increased with increasing intensity and duration of water stress. However, IAA content of shattercane leaves did not demonstrate a similar trend.

Epicuticular wax content increased due to water stress treatments in both species, suggesting significant plant responses to environmental alterations.

The experimental procedure to generate water stress described in this paper showed some limitations to control of small increments of water stress. However, the system provided the flexibility to subject a large number of plants to a specified stress condition.

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SECTION II. NICOSULFURON AND PRIMISULFURON-METHYL ACTIVITY ON, UPTAKE BY, AND TRANSLOCATION IN SHATTERCANE (*Sorghum bicolor* [L.] Moench) AND WOOLLY CUPGRASS (*Eriochloa villosa* [Thunb.] Kunth) GROWN UNDER WATER STRESS

Introduction

Shattercane and woolly cupgrass are important and expanding weeds in agroecosystems of the Midwestern states (Bello, 1988; Fawcett, 1980; Owen, 1987; Strand and Miller, 1980). Both grasses demonstrate remarkable weedy characteristics such as a rapid growth rate, high reproductive capacity, seed dormancy, and are difficult to control with conventional methods (Fawcett, 1980; Martin, 1986; Nilson et al., 1988).

Modern agricultural production relies on the correct combination of crops, environmental variables, and agronomic technologies for efficient food production. Water is the environmental resource most limiting to crop production in United States. Considering the total agricultural land of United States and the world, 25% show some degree of water limitation (Boyer, 1982).

When environmental variables limit crop production, losses occur due to direct and indirect factors. Direct crop losses due to water stress are mainly expressed as a

yield reduction. The level of yield reduction is a function of three variables: drought duration, drought intensity, and crop phenological stage. Indirect crop losses are due to the lack of consistent agronomic practices for crop production under water stress.

The use of postemergence herbicides is increasing under specific agronomic conditions such as reduced or no-tillage production systems or for the management of troublesome weeds. Postemergence herbicides are active after a successful chain of events. After herbicide deposition on the plant surface, the herbicide must be absorbed into the plant and transported to the action site. At the action site, the herbicide must be present in a chemically active form, at a concentration equal to or greater than a threshold amount, and for an adequate period of time to produce the toxic effect.

Nicosulfuron [2-[[(4,6-dimethoxypyrimidin-2-yl) aminocarbonyl]aminosulfonyl]-N,N-dimethyl-3-pyridinecarboxamide], and primisulfuron-methyl [3-[4,6-bis-(difluoromethoxy)-pyrimidin-2-yl]-1-(2-methoxycarbonylphenylsulfonyl)urea], are new sulfonylurea herbicides that present promising features for the control of shattercane (Maurer et al., 1987) and woolly cupgrass through postemergence application to corn (Kuratle et al., 1988; Porpiglia et al., 1988). The new products are highly

selective, have exceptional herbicide activity at very low rates, and have demonstrated very low toxicity to mammals (Ciba-Geigy, 1989; DuPont, 1989). These characteristics are environmentally attractive and represent a potential for minimal environmental pollution from these herbicides.

Crops and weeds growing under water stress conditions suffer morphological and physiological changes that may affect the efficacy of postemergence herbicides (Ahmadi et al., 1980; Akey and Morrison, 1983; Dastgheib et al., 1990; Kloppenburg and Hall, 1990; Kidder and Behrens, 1988; Peregoy et al., 1990; Waldecker and Wyse, 1985). Postemergence herbicide application to plants under water stress conditions demonstrate variable and unpredictable results. The causes of poor herbicidal control of weeds under water stress are not clearly understood, but are presumed to be related with interferences in herbicide absorption, translocation, or metabolism. No available reports specifically described the activity of nicosulfuron and primisulfuron-methyl in shattercane and woolly cupgrass plants under water stress.

The objective of this study was to determine the effect of differential plant water status on activity, uptake, and translocation of sulfonylurea herbicides in shattercane and woolly cupgrass.

Materials and Methods

General Procedures

The growth media was a mix of 80:20 (v/v) of soil and sand. The soil moisture characteristics curve for the growth media was determined with a tension table in the low suction range (0.0 to 0.1 MPa) and with a ceramic pressure plate apparatus in the high suction range (0.1 to 1.5 MPa). The desorption data were used to solve the Van Genuchten equation thus describing the relationship between matric potential and the volumetric soil water potential (Van Genuchten, 1980) using non-linear regression techniques. Figure 5 shows the volumetric water content plotted against the matric suction of the growth medium.

Round plastic pots, 11 cm of diameter and 10 cm tall with a volume of 500 ml, were filled with 450 g of the dry growth medium. Three seeds of shattercane or woolly cupgrass were planted in each pot and three days after emergence, plants were thinned to 1 plant/pot. Seeds were collected from a natural shattercane population in Dallas Center, Iowa and a woolly cupgrass population in Stratford, Iowa. Pots were transferred to growth chambers (CW 36 Conviron Products Co., Winnipeg, Manitoba, Canada) and the soil moisture was maintained near field capacity with a drip irrigation system.

Environmental conditions for the growth chamber were 16 hrs day and 8 hrs night. Figure 6 shows the daily course of temperature. Relative humidity was maintained at 85% and the photosynthetic photon flux density (PPFD) at the top of the canopy as provided by a combination of fluorescent and incandescent lamps, was 500 μmol m^{-2} s^{-1}. Plants were watered weekly with 40 ml of a solution containing 3.1 g of soluble fertilizer/L (20-20-20 ($N-P_2O_5-K_2O$), W. R. Grace & Co-Conn., Fogelsville, PA).

In an initial experiment to test the plant age effect on herbicide efficacy, plants were subjected to different levels of soil water potential for 8 days beginning 14 or 21 days after emergence. Herbicide application was made at the end of the water stress period. Pots were weighed twice daily and water added to the soil thus maintaining the appropriate level of soil water potential. Water was added to the soil with a syringe equipped with a 10 cm needle with lateral perforations to distribute water throughout the total pot volume. Pots were arranged in blocks and the blocks randomly assigned to one of the four soil water potential treatments (-0.03, -0.4, -0.8, and -1.2 MPa).

For the herbicide uptake and translocation experiments, the experimental conditions were similar to those described above, but herbicides were applied to plants 28 days after emergence.

Herbicide Activity Experiments

Herbicide efficacy was determined using a split-split plot experimental design with three replications. Plant age was the main plot, levels of soil water potential was the split plot, and herbicide rate was the split-split plot. Each plot was composed of 6 plants grown either 14 or 21 days under well-watered conditions, followed by 8 days of different levels of soil water potential. Plants were randomly assigned to one of the four previously described soil water potential treatments. Herbicide application was made at the end of the water stress period (22 or 29 days after emergence, respectively).

Two rates were applied for each herbicide; 17.5 and 35.0 g of active ingredient (a.i.) ha^{-1} of nicosulfuron, and 20.3 and 40.6 g a.i. ha^{-1} of primisulfuron-methyl. Experiments with shattercane included both herbicides while woolly cupgrass experiments included only nicosulfuron. Field observations suggested that primisulfuron-methyl was not effective on woolly cupgrass (Owen et al., 1989). Commercial herbicide formulations were applied with a laboratory sprayer using a single flat-fan nozzle (8001EVS) at 124 kPa pressure and delivering 234 L ha^{-1} of spray volume.

All the pots were watered to field capacity immediately after herbicide application. Herbicide toxicity was

evaluated at 7, 14, and 28 days after treatment (DAT). Herbicide efficacy was rated in a 0 to 100 visual scale, with 0 = no injury and 100 = total injury. Plant injury evaluations were based on evaluation of sulphonylurea main symptoms: reduced plant growth, enhanced anthocyanin formation, loss of leaf nyctinasty, abscission, vein discoloration, terminal bud death, chlorosis, and necrosis (Beyer et al, 1988). ANOVA analyses were conducted using the efficacy values of 28 days. At seven days after herbicide application, 4 plants from each treatment were harvested and dry weight was determined after drying the plants in an oven at 65 C for 24 hrs. This experiment evaluated the effect of the herbicide and rate on plant growth and was repeated.

Herbicide Uptake and Translocation

Herbicide uptake and translocation of nicosulfuron and primisulfuron-methyl was determined with ^{14}C-labeled herbicides. Plants were sprayed with commercial herbicide (17.5 g a.i. ha^{-1} of nicosulfuron, and 20.3 g a.i. ha^{-1} of primisulfuron-methyl) 1 hour prior to the application of the ^{14}C-herbicide. Radiollabeled herbicide was applied to the adaxial leaf surface with a microsyringe (5 droplets of 2 μl) on the central part of the last fully expanded leaf. The ^{14}C-nicosulfuron used had specific activity 62.9 $\mu Ci\ mg^{-1}$, a

^{14}C-nicosulfuron used had specific activity 62.9 μCi mg^{-1}, a radiochemical purity of 99.0%, and the ^{14}C-label was located in the pyridine-2-^{14}C. The herbicide was synthesized by Ishihara Sangyo (DuPont Company, Wilmington, Delaware). The ^{14}C-primisulfuron-methyl used had specific activity 56.2 μCi mg^{-1}, a radiochemical purity of 96.7%; chemical purity as determined by HPLC of 98.9%, and was synthesized by Ciba-Geigy (Ciba-Geigy Corporation, Greensboro, North Carolina).

The ^{14}C-herbicides were diluted with 1 ml of tetrahydrofuran and mixed with 10 ml of unlabelled formulated herbicide to give a final rate of 17.5 g a.i. ha^{-1} of nicosulfuron and 20.3 g a.i. ha^{-1} of primisulfuron-methyl; the addition of 0.1% (v/v) of X-77 non-ionic surfactant (X-77 Spreader. Chevron Chem. Co., Richmond, CA) resulted in the desired concentration (10,000 counts per minute cpm/μl^{-1}).

Plants were harvested at 24, 48, 96, and 192 hours after treatment (HAT). Plants were separated into treated leaves and untreated portions of the plant. In the treated leaves, the unabsorbed herbicide was determined by washing the leaf surface three times with 5 ml of 10% (v/v) ethanol:water collected in a 20 ml scintillation vial to which 12 ml of scintillation cocktail (Ready Safe, Beckman Instruments, Inc., Fullerton, CA) was added. The ^{14}C content was quantified as counts per minute (cpm) by liquid scintillation spectrometry (Devine et al., 1984). The same amount of

herbicide was applied to glass microscope cover slips. After drying, the cover slips were washed using the method described above, and ^{14}C determined using liquid scintillation spectrometry. Most of the herbicide (98%) was recovered by this technique.

Herbicide sequestered in the cuticle was determined by dipping the treated area of the leaf in 20 ml of chloroform for 30 seconds. Chloroform was evaporated and 10 ml of scintillation cocktail were added to the scintillation vial. The ^{14}C activity was quantified as cpm by liquid scintillation spectrometry.

Remaining leaves and plants were immediately frozen in liquid nitrogen, oven dried at 65 C for 24 hrs, weighed, ground, and a 500 mg aliquot (or the entire sample if less than 500 mg) was combusted (Packard Tri-Carb sample oxidizer, model 306, Packard Instrument Co., Downers Grove, IL). The $^{14}CO_2$ was trapped on carbon dioxide absorber (Carbo-Sorb, 2-methoxyethylamine, Packard Instrument Co., Downers Grove, IL) and scintillation cocktail [Permafluor V (a blend of scintillators PPO and bis-MSB in toluene and methanol), Packard Instrument Co., Downers Grove, IL]. The radioactivity was determined as cpm by liquid scintillation spectrometry. If the sample was larger than 500 mg, the measured radioactivity was recalculated to accommodate the

total plant weight. The experimental design was a split-plot design with the water stress treatment as the main plot and the time of radioactivity recovery after herbicide application as the split-plot. Every fraction was analyzed separately.

Results and Discussion

Herbicide Activity

Due to the slow speed of activity of these herbicides, data will refer to plant injury at 28 DAT. Plant age, soil water potential and the herbicide treatment affected shattercane control (Table 11, in the Appendix). There were significant interactions between plant age and soil water potential, and between soil water potential and herbicide. The highest level of shattercane control was observed on 22 day-old plants grown under well-watered conditions, averaged over all the herbicide treatments. Increasing plant age or decreasing herbicide rates decreased shattercane control (Figure 31). Maurer (1987), reported decreasing activity of primisulfuron-methyl on shattercane with increasing plant age.

Considering the interaction between soil water potential and herbicide treatment, results indicated that the greatest herbicide efficacy on shattercane occurred when plants were

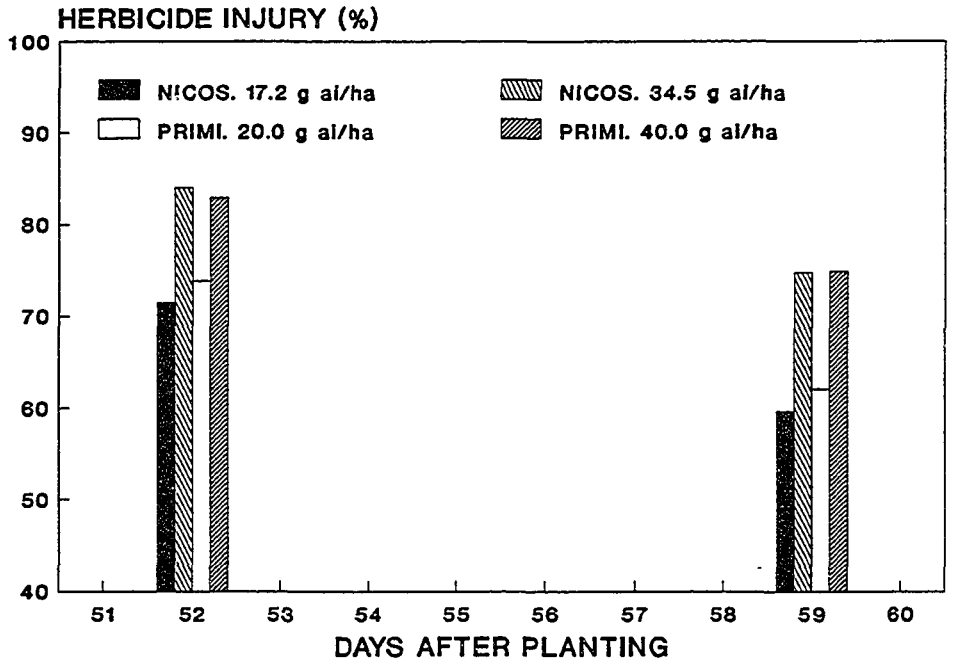

Figure 31. Herbicide efficacy on shattercane plants as affected by plant age. Efficacy was evaluated 28 days after treatment. Injury was rated on a 0 to 100 scale, with 0 = no injury and 100 = plant death. Each data point represents the average of 12 means

well-watered and the higher herbicide rates were used, when averaged over plant age treatments. Decreasing soil water potential or herbicide rate decreased herbicide efficacy on shattercane (Figure 32).

Plant age, soil water potential, the interaction between plant age and soil water potential, herbicide rate, and the interaction between soil water potential and herbicide rate, were component variables affecting the herbicide

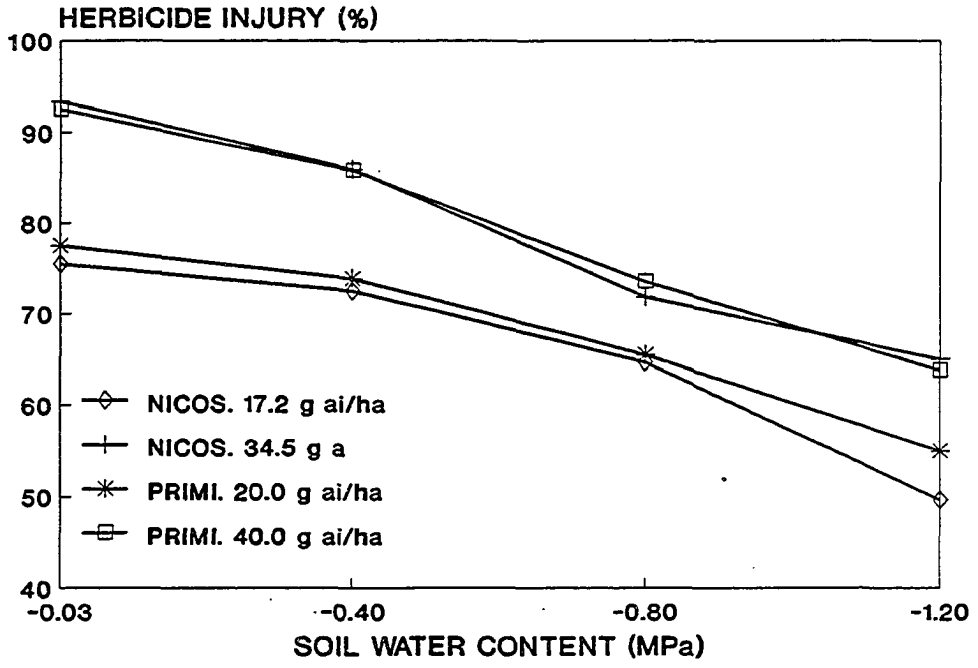

Figure 32. Herbicide efficacy on shattercane plants grown at different soil water potential. Herbicide toxicity was evaluated at 28 days after treatment. Injury was rated on a 0 to 100 scale, with 0 = no injury and 100 = plant death. Each data point represents the average of 6 means

efficacy on woolly cupgrass (Table 12 in the Appendix). The highest efficacy on woolly cupgrass was observed on 22 day-old plants grown under well water conditions. Increasing plant age averaged over all herbicide and soil water potential treatments decreased weed control (Figure 33). Observations of this study suggest that woolly cupgrass has a narrower 'application window' than shattercane.

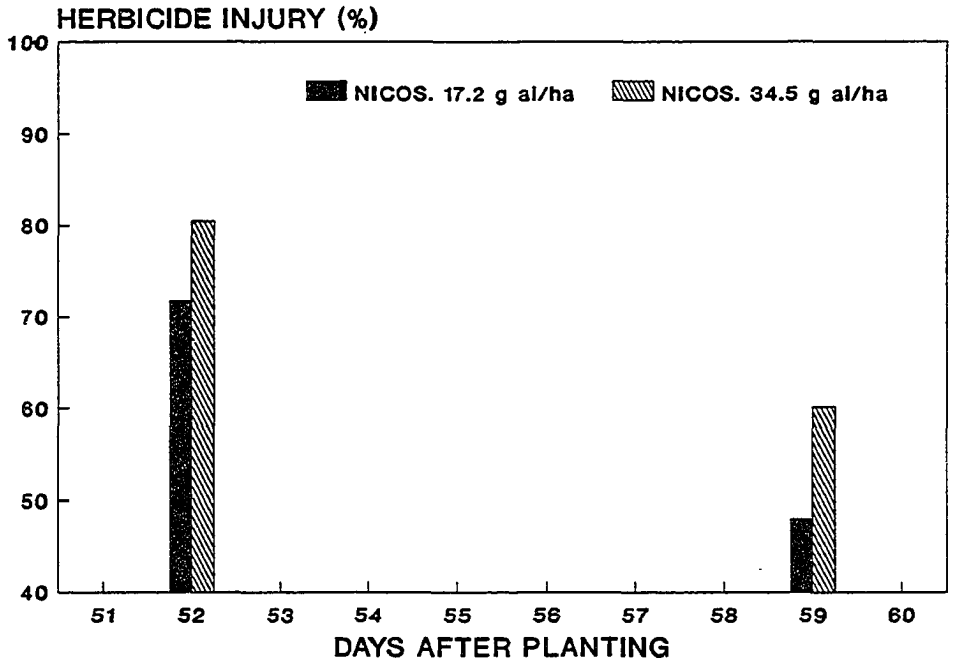

Figure 33. Herbicide efficacy on woolly cupgrass plants. as affected by plant age. Efficacy was evaluated 28 days after treatment. Injury was rated on a 0 to 100 scale, with 0 = no injury and 100 = plant death. Each data point represents the average of 12 means

Highest herbicide efficacy was observed under well watered conditions and with the high rate of nicosulfuron (Figure 34).

Plant dry weight results of shattercane and woolly cupgrass indicated that growth ceased one week after herbicide application (not reported). Additional observations (not reported) indicated that in the week

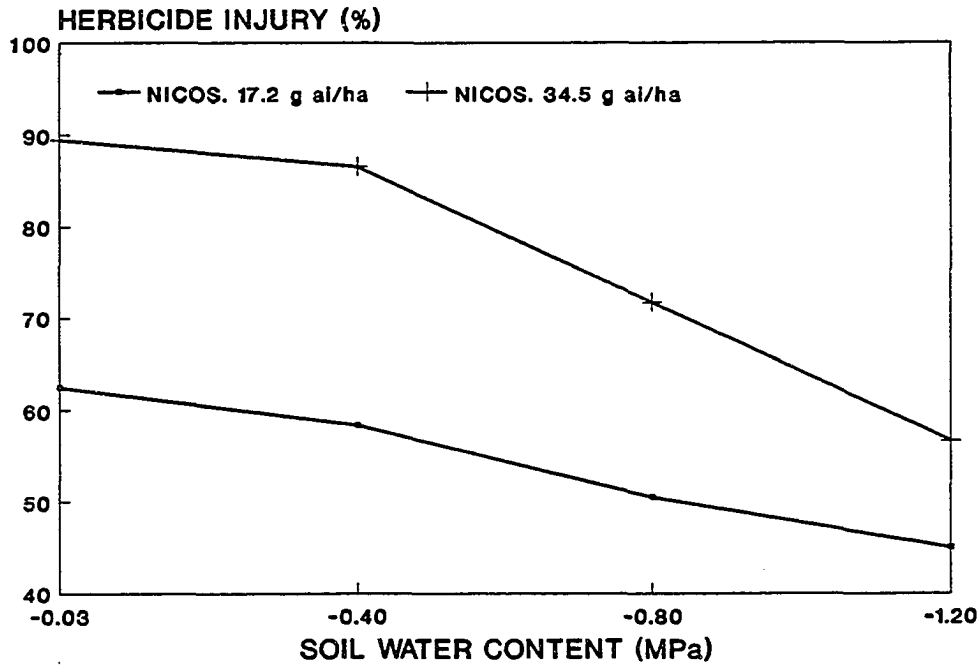

Figure 34. Herbicide efficacy on woolly cupgrass plants grown at different soil water potential. Herbicide injury was evaluated at 28 days after treatment. Injury was rated on a 0 to 100 scale, with 0 = no injury and 100 = plant death. Each data point represents the average of 6 means

following herbicide application, photosynthetic rate and stomatal conductance remained unaltered. All this information confirms the fact that both herbicides demonstrated slow phytotoxicity on shattercane and woolly cupgrass.

It is interesting to note the conflict between the earlier herbicide application time, as documented by this study, and the ecological consideration that these weeds have the capacity for later germination flushes during

the season. In practice, farmers may delay the herbicide application time in an attempt to control several weed flushes. These data indicate that the herbicide will be less effective under such conditions.

Herbicide Uptake and Translocation

Percentage of different fractions of recovered radiolabel herbicide (unabsorbed, sequestered in the cuticles, taken into the treated leaf, and translocated to other plant tissues) for each weed species are shown in Table 6 and 7. Soil water potential had no effect on the amount of herbicide remaining on the leaf surface of shattercane when averaged across harvest times. Averaging both herbicides across harvest times, the herbicide remaining on the leaf surface was 42, 39, 37, and 40% of the total herbicide applied for the -0.03, -0.4, -0.8, and -1.2 MPa soil water potential treatments, respectively.

Highly significant differences in absorption between herbicides were observed in shattercane (Table 13 in the Appendix). Averaging across soil water potential and harvest time treatments, more primisulfuron-methyl remained unabsorbed than nicosulfuron (47 and 31% of the total herbicide applied, respectively). Molecular differences in polarity between these compounds are most likely the explanation of the results.

Table 6. Percentage of radiolabel herbicide recovered in different fractions of shattercane at various harvest times[a]

Soil water potential	Nicosulfuron (%)				Primisulfuron-methyl (%)			
	Hours after treatment							
	24	48	96	192	24	48	96	192
-0.03 MPa								
Unabsorbed	47	30	36	19	60	55	52	33
Epicutic. wax	24	22	25	24	14	13	18	16
Leaf uptake	21	29	26	32	17	20	21	30
Translocated	6	10	12	20	5	8	8	12
-0.4 MPa								
Unabsorbed	43	25	27	26	57	53	46	31
Epicutic. wax	21	25	25	38	13	13	19	22
Leaf uptake	15	24	28	22	14	17	21	23
Translocated	4	8	8	10	4	8	7	8
-0.8 MPa								
Unabsorbed	37	27	31	20	59	44	43	31
Epicutic. wax	22	27	30	51	13	22	22	21
Leaf uptake	15	18	21	20	13	12	14	19
Translocated	3	6	7	5	4	5	6	7
-1.2 MPa								
Unabsorbed	39	27	30	29	60	50	44	39
Epicutic. wax	23	30	33	38	13	16	19	20
Leaf uptake	13	16	18	18	11	10	11	14
Translocated	2	4	6	6	2	4	5	7

[a]Each value is the average of two samples.

Table 7. Percentage of radiolabel herbicide recovered in different fractions of woolly cupgrass at various harvest times[a]

Soil water potential	Nicosulfuron (%)				Primisulfuron-methyl (%)			
	Hours after treatment							
	24	48	96	192	24	48	96	192
-0.03 MPa								
Unabsorbed	27	23	21	28	42	37	32	22
Epicutic. wax	28	35	37	33	24	25	22	25
Leaf uptake	19	24	25	21	19	23	25	23
Translocated	10	13	13	14	7	8	11	13
-0.4 MPa								
Unabsorbed	33	23	27	29	42	39	28	23
Epicutic. wax	30	36	30	38	21	22	26	28
Leaf uptake	16	19	20	20	19	21	20	21
Translocated	11	10	7	8	6	7	8	11
-0.8 MPa								
Unabsorbed	39	20	27	33	43	41	28	22
Epicutic. wax	23	36	40	42	22	22	27	23
Leaf uptake	10	15	19	18	15	16	17	16
Translocated	6	7	7	6	4	6	6	9
-1.2 MPa								
Unabsorbed	39	23	23	34	49	37	36	27
Epicutic. wax	30	40	37	39	16	24	24	25
Leaf uptake	10	13	13	14	13	13	12	12
Translocated	4	5	5	4	3	5	5	7

[a]Each value is the average of two samples.

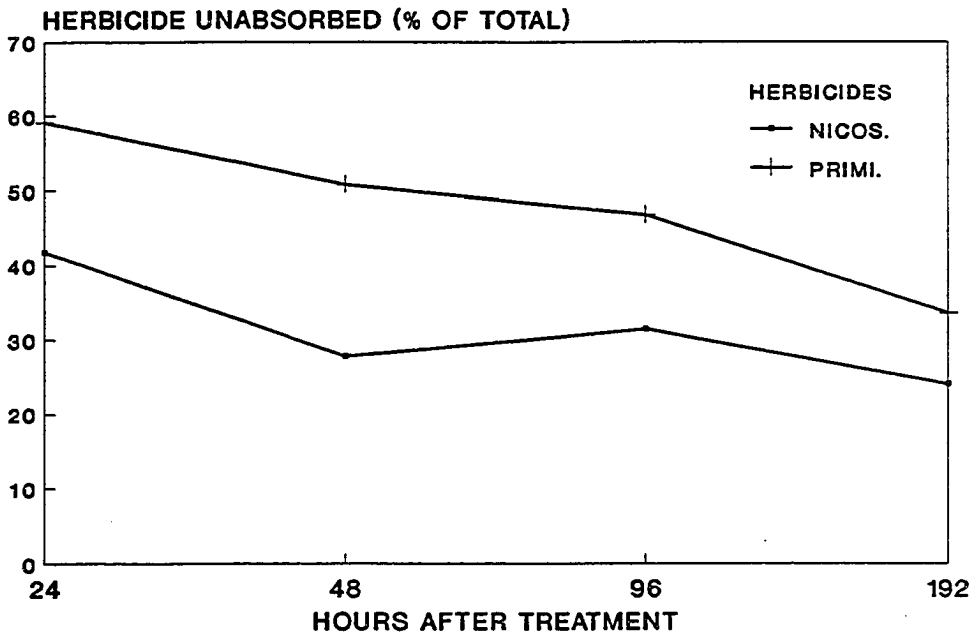

Figure 35. Herbicide unabsorbed by shattercane leaves as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

A significant interaction between harvest time and herbicide absorption was observed for shattercane (Figure 35 and Table 13 in the Appendix). Plants in this experiment were watered by drip irrigation, so no herbicide should have been washed off the leaf by watering. Both herbicides continued to be absorbed as time after application increased. However, maximum absorption occurred during the initial 24 h after application.

A significant effect of water stress treatment on the herbicide absorption (averaged across harvest times and herbicides) was detected for woolly cupgrass. Twenty-nine, 31, 32, and 33% of the herbicide remained unabsorbed for -0.03, -0.4, -0.8, and -1.2 MPa soil water potential treatments respectively.

Averaging across soil water potential and harvest time treatments, differences in herbicide penetration between nicosulfuron and primisulfuron-methyl were also detected in woolly cupgrass (Table 14 in the Appendix). More primisulfuron-methyl remained unabsorbed than nicosulfuron (34 and 28% of the total herbicide applied, respectively).

Herbicide absorption by woolly cupgrass continued with time after application as long as 48 hrs for nicosulfuron and 192 hrs for primisulfuron-methyl. In the initial 24 hrs, 66% of the total nicosulfuron was absorbed as compared with 56% of primisulfuron-methyl (Figure 36).

Experimental evidence supports epicuticular waxes as the main barrier impeding herbicide movement into the plant foliage (Riederer and Schonherr, 1984). No differences in the amount of herbicide present in shattercane leaf cuticles were found due to water stress treatments, as a function of time after application (Table 15 in the Appendix). However, differences in cuticular absorption were significant between

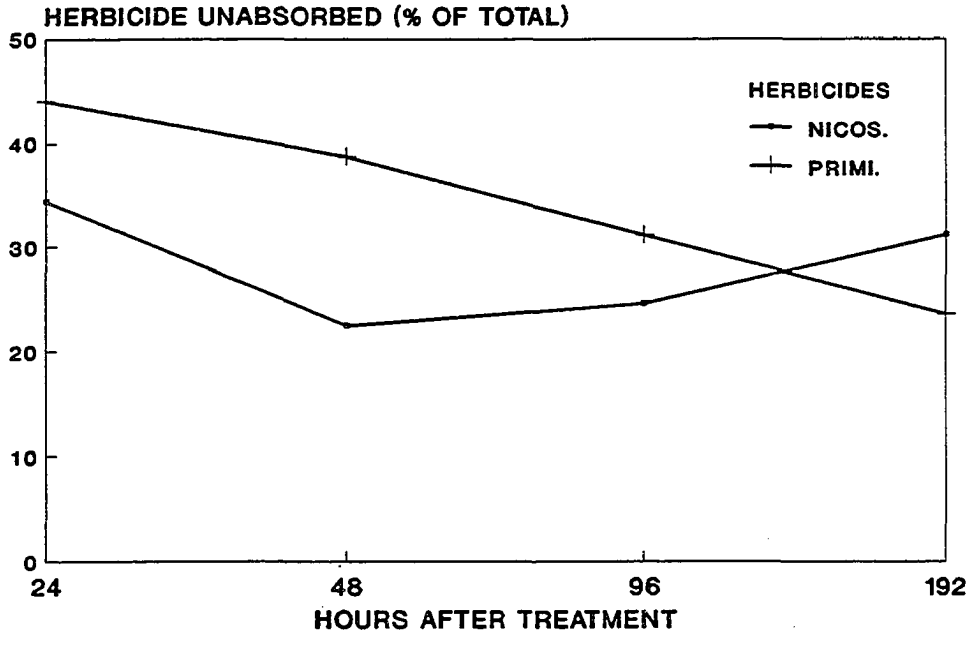

Figure 36. Herbicide unabsorbed by woolly cupgrass leaves as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

herbicides and harvest times. Both herbicides accumulated in shattercane cuticles (Figure 37) but more nicosulfuron than primisulfuron-methyl remained trapped (29 and 17%, respectively).

An absorption pattern similar to shattercane was observed in woolly cupgrass cuticles. No differences were found for cuticular absorption due to water stress treatments (Table 16 in the Appendix).

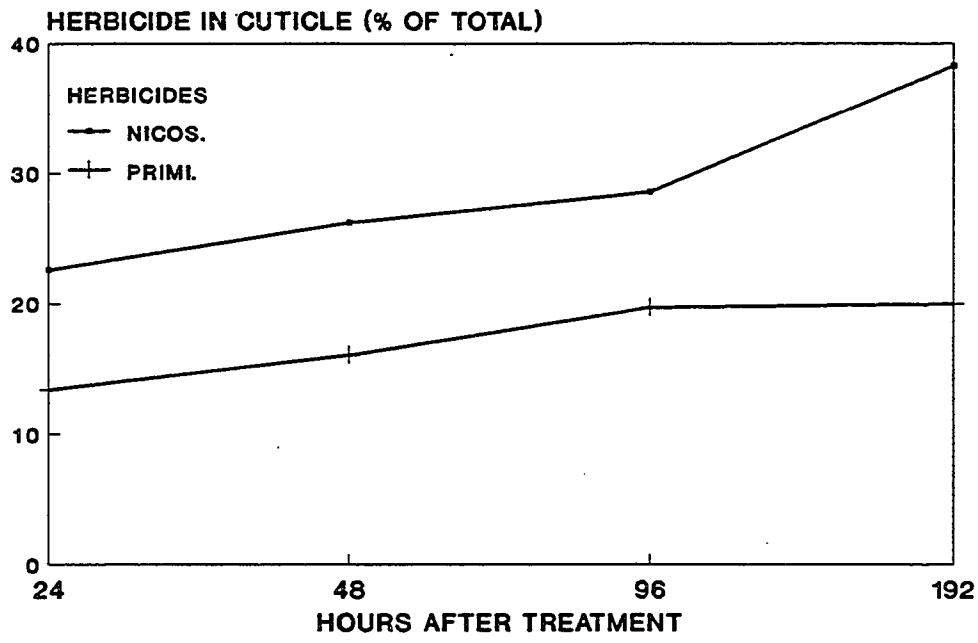

Figure 37. Herbicide content in shattercane leaf cuticles as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

Data demonstrated that both herbicides accumulated in cuticles during the interval of the experiment (Figure 38). The two herbicides were retained differently in woolly cupgrass cuticles. Averaged across all harvest times, more nicosulfuron than primisulfuron-methyl (35 and 24% of the total, respectively) was retained.

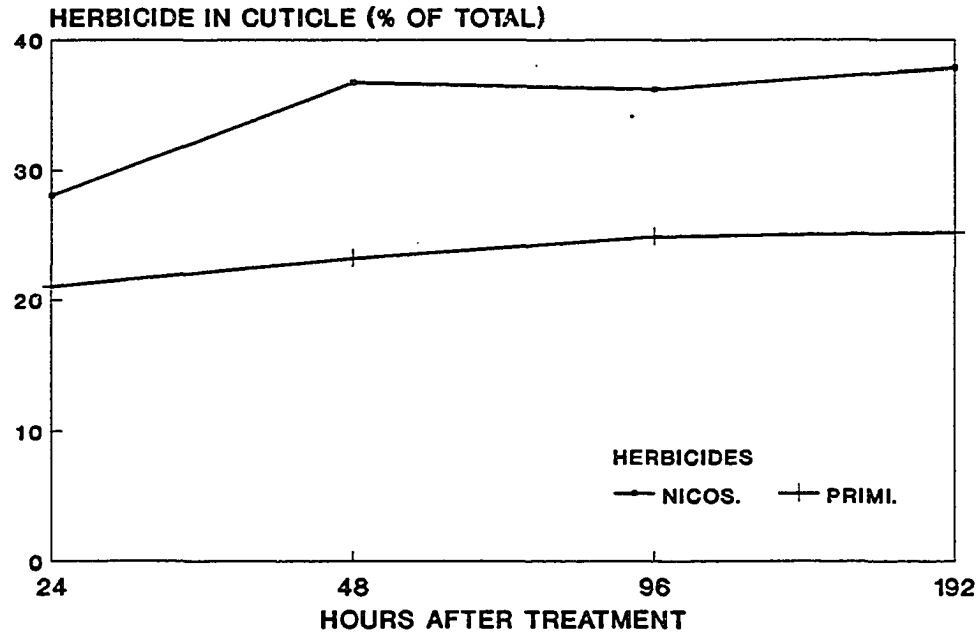

Figure 38. Herbicide content in woolly cupgrass leaf cuticles as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

Differential herbicide penetration across the plant cuticle and distinct retention in epicuticular wax layers may be due to the dynamic interaction between physico-chemical properties of the active ingredient, environmental factors, and plant factors such as: epicuticular wax thickness and chemical composition (Graham-Bryce, 1984).

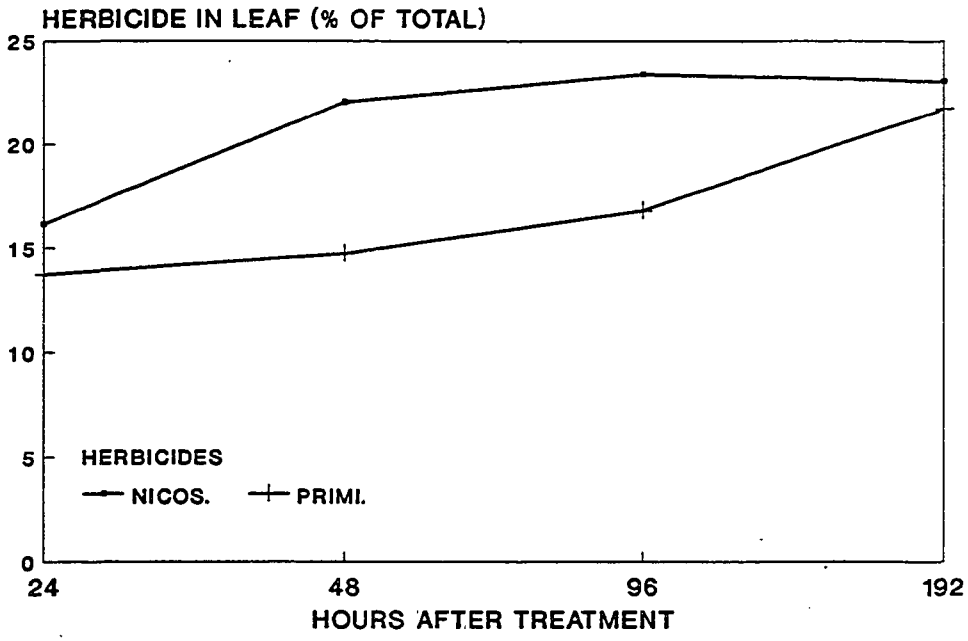

Figure 39. Herbicide content inside shattercane leaves as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

Highly significant differences in herbicide penetration inside the treated leaf were observed in shattercane (Table 17 in the Appendix). A significant effect of soil water potential, herbicides, and time after application was detected. Increasing the water stress decreased the herbicide absorption. Averaging both herbicides across harvest times, the herbicide inside leaves was 24, 21, 16, and 14% of the total herbicide applied for the -0.03, -0.4, -0.8, and -1.2 MPa soil water potential treatments,

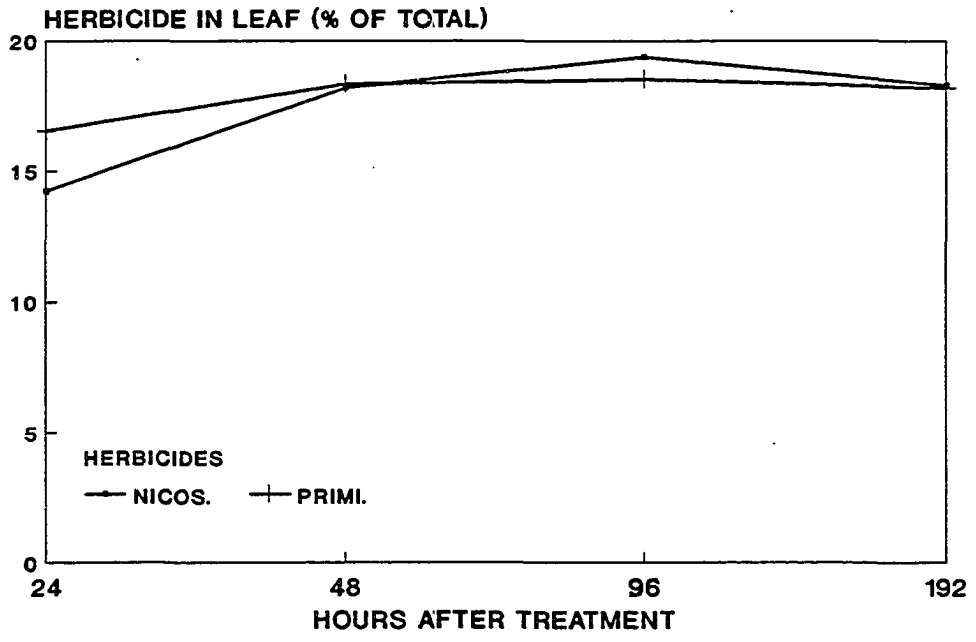

Figure 40. Herbicide content inside woolly cupgrass leaves as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

respectively. Averaging across soil water potential and harvest times, more nicosulfuron than primisulfuron-methyl was absorbed by shattercane leaves (21 and 16% of the total herbicide applied, respectively). Herbicide accumulation inside leaves increase with time after application (Figure 39).

Herbicide absorption by woolly cupgrass leaves was significantly affected by soil water stress (Table 18 in the Appendix). Averaging both herbicides across harvest times, the herbicide inside treated woolly cupgrass leaves was 22,

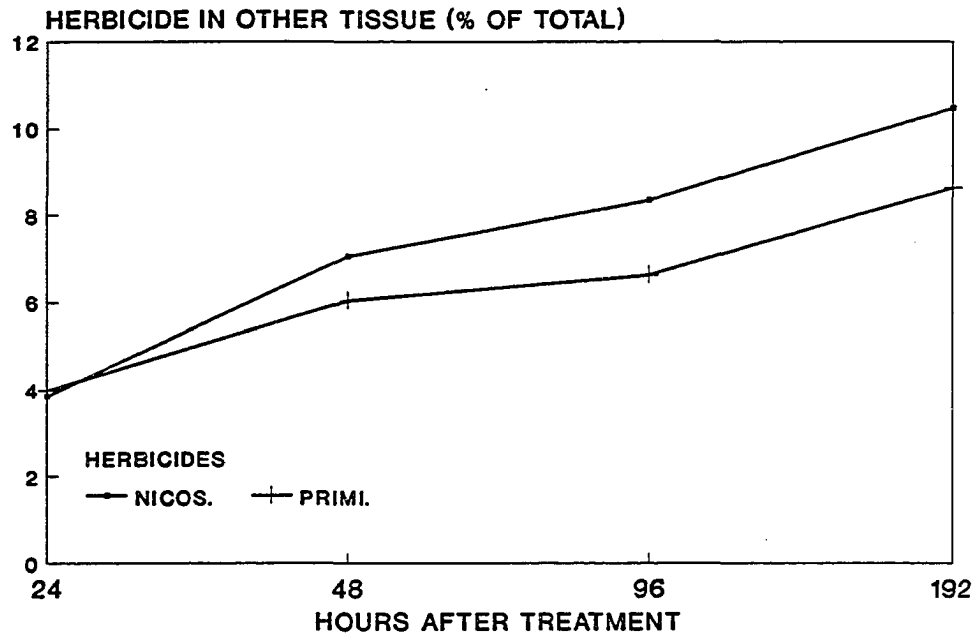

Figure 41. Herbicide translocation to untreated areas of shattercane plants as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

19, 16, and 13% of the total herbicide applied for the -0.03, -0.4, -0.8, and -1.2 MPa soil water potential treatments, respectively. Accumulation of radiolabel herbicide inside treated woolly cupgrass leaves is demonstrated in Figure 40.

Herbicide translocation represented a small fraction of the total herbicide applied in both species. Between 4 to 11% of the total herbicide applied was recovered in other tissues (Table 6 and 7). The total amount of herbicides translocated from treated leaves to other plant tissues

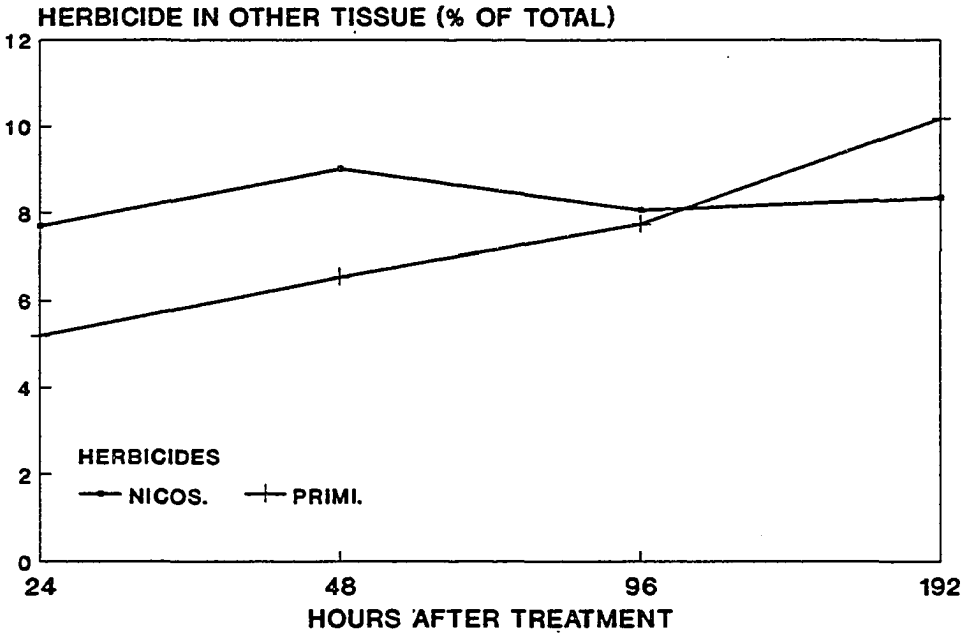

Figure 42. Herbicide translocation to untreated areas of woolly cupgrass plants as a function of time (expressed as percent of the total applied). Each data point represents the average of 8 means

increased with time after application.

Soil water potential had a significant effect on translocation of both herbicides in shattercane (Table 19 in the Appendix). Averaging both herbicides across harvest times, maximum herbicide translocation was observed in shattercane plants growing under well-watered conditions. No differences in herbicide translocation were observed between plants growing at -0.4 or -0.8 MPa of soil water potential.

The lowest herbicide translocation was observed in plants growing at -1.2 MPa. The significant evolution of herbicide translocation with time is demonstrated in Figure 41.

Soil water potential was the only variable affecting herbicide translocation in woolly cupgrass plants (Table 20 in the Appendix). Averaging both herbicides across harvest times, the herbicide translocated was 11, 9, 7, and 5% of the total herbicide applied for the -0.03, -0.4, -0.8, and -1.2 MPa soil water potential treatments, respectively. Maximum herbicide translocation was observed in plants growing under well-watered conditions, and minimum translocation was measured for plants growing at -1.2 MPa of soil water potential. Herbicide translocation with time is demonatrated in the Figure 42.

In woolly cupgrass plants, both herbicides were absorbed and translocated in equivalent amounts, however the lack of activity of primisulfuron-methyl on woolly cupgrass may be related with subsequent metabolization of the herbicide.

Conclusions

The results of these studies demonstrated that nicosulfuron and primisulfuron-methyl activity on shattercane and woolly cupgrass were affected by several factors. Herbicide activity was maximum on well-watered shattercane and woolly cupgrass plants. Increasing plant water stress reduced herbicide activity in both species.

Plant age was an important variable affecting herbicide injury. Increasing shattercane and woolly cupgrass age reduced herbicide activity. Results suggest that woolly cupgrass has a more limited application window (more age dependent) than shattercane. Herbicide rate was linearly linked with herbicide activity for both compounds.

Herbicide activity was slow for both compounds. Weed growth stopped during the week after herbicide application. However, photosynthetic rate and stomatal conductance are not affected in the same time period. Visual injury symptoms appeared 10 DAT, but complete plant desiccation occurred after 20 DAT.

Shattercane uptake of nicosulfuron and primisulfuron-methyl was not affected by soil water potential treatment. Uptake of both compounds increased with time, but the maximum absorption occurred in the initial 24 hrs. More primisulfuron-methyl than nicosulfuron remained unabsorbed on shattercane leaf surfaces. Water stress treatments did not

affect cuticular herbicide retention in shattercane plants. Both herbicides accumulated in the cuticle with time. More nicosulfuron remained trapped in cuticles than primisulfuron-methyl.

Soil water potential affected the uptake of nicosulfuron and primisulfuron-methyl by woolly cupgrass. Plants under water stress absorbed less herbicide than well-watered plants. More primisulfuron-methyl remained unabsorbed, but more nicosulfuron remained in woolly cupgrass cuticles.

Observed differences in uptake and cuticular retention were not big enough to explain reduced herbicide activity on water stressed plants. Additionally, observed differences in uptake and cuticular retention were most likely due to interactions between physico-chemical properties of the compounds and some physico-chemicals properties of plant membranes.

The total amount of herbicide translocated from the application area to other plant tissues under the conditions of this study was reduced. Clearly, soil water potential significantly affected herbicide translocation in shattercane and woolly cupgrass.

Under the conditions of this study, the lack of activity of sulfonylurea herbicides when applied to water stressed plants was related with highly significant translocation reduction.

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APPENDIX

Table 1. Means and standard deviations of dry weight (DW) and leaf area (LA) of shattercane and woolly cupgrass growing without water stress

Days after emergence (DAE)	DW[a] means	DW[a] Std.	LA[b] means	LA[b] Std.
Shattercane				
4	0.14	0.06	32	9.13
8	0.28	0.16	53	7.31
12	0.58	0.13	85	10.29
16	0.90	0.15	151	39.16
20	1.35	0.20	225	22.92
24	1.93	0.39	301	21.85
28	2.64	0.34	382	19.15
32	3.58	0.45	473	38.96
Woolly cupgrass				
4	0.12	0.06	25	4.94
8	0.21	0.05	48	13.65
12	0.43	0.15	94	19.37
16	0.87	0.17	164	17.29
20	1.29	0.18	229	17.84
24	2.50	0.72	303	20.79
28	3.92	0.58	392	16.76
32	4.98	0.73	491	35.80

[a]Dry weights are expressed in g/plant, each value is the average of five plants.

[b]Leaf area are expressed in cm^2/plant, each value is the average of five plants.

Table 2. Analysis of variance of MGR of shattercane

Source of variation	df	Mean square	F value	P > F
Block (B)	2	0.00217914	2.36	0.1371
Water (W)	3	0.35538818	360.81	0.0001
B*W Error (a)	6	0.00196994	0.71	0.6486
Sampling time (T)	2	0.00005689	0.06	0.9407
B*T	4	0.00344035	1.86	0.1825
W*T	6	0.00615485	2.22	0.1133
Error	12	0.00555096		
Corrected Total	35	0.37474030		

Table 3. Analysis of variance of MGR of woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	0.00214362	0.85	0.4500
Water (W)	3	0.39116036	71.96	0.0001
B*W Error (a)	6	0.01087158	1.44	0.2764
Sampling time (T)	2	0.00591124	2.36	0.1371
B*T	4	0.00121559	0.24	0.9089
W*T	6	0.03082940	4.10	0.0181
Error	12	0.01505697		
Corrected Total	35	0.45718876		

Table 4. Analysis of variance of MLAER of shattercane

Source of variation	df	Mean square	F value	P > F
Block (B)	2	0.00452739	0.42	0.6644
Water (W)	3	0.17421873	49.97	0.0001
B*W Error (a)	6	0.00348629	0.33	0.9108
Sampling times (T)	2	0.00270982	0.25	0.7803
B*T	4	0.01145439	1.07	0.4132
W*T	6	0.01256450	1.17	0.3813
Error	12	0.01070094		
Corrected Total	35	0.80766413		

Table 5. Analysis of variance of MLAER of woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	0.00056589	0.07	0.9323
Water (W)	3	0.15168298	66.66	0.0001
B*W Error (a)	6	0.00227553	0.28	0.9337
Sampling time (T)	2	0.00501938	0.63	0.5515
B*T	4	0.00272195	0.34	0.8463
W*T	6	0.00855479	1.07	0.4332
Error	12	0.00802348		
Corrected Total	35	0.63837099		

Table 6. Means and standard deviations of leaf water potential of shattercane plants subjected to different soil water potential treatment

Time	Leaf water potential[a] Means (Std. dev.) -0.03 MPa	-0.4 MPa	-0.8 MPa	-1.2MPa
Shattercane				
5:00	-0.1(0.01)	-0.6(0.02)	-1.1(0.04)	-1.3(0.03)
8:00	-0.6(0.01)	-0.8(0.03)	-1.6(0.04)	-2.3(0.06)
11:00	-0.8(0.02)	-1.3(0.04)	-2.1(0.06)	-3.1(0.08)
14:00	-1.0(0.03)	-1.9(0.04)	-2.3(0.08)	-3.5(0.08)
17:00	-0.6(0.01)	-0.8(0.03)	-1.4(0.05)	-1.8(0.05)
20:00	-0.5(0.03)	-1.2(0.03)	-1.7(0.04)	-2.9(0.07)
Woolly cupgrass				
5:00	-0.1(0.01)	-0.5(0.02)	-0.9(0.03)	-0.9(0.02)
8:00	-0.7(0.02)	-0.9(0.02)	-1.1(0.02)	-1.9(0.04)
11:00	-0.9(0.02)	-1.1(0.03)	-1.9(0.04)	-2.7(0.07)
14:00	-1.2(0.02)	-1.7(0.04)	-2.1(0.03)	-3.1(0.09)
17:00	-0.8(0.02)	-1.1(0.02)	-1.4(0.04)	-2.1(0.07)
20:00	-0.5(0.01)	-1.3(0.02)	-1.5(0.03)	-2.4(0.03)

[a]Leaf water potentials are expressed in MPa, each value is the average of five plants.

Table 7. Analysis of variance of stomatal conductance of shattercane and woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	855	3.50	0.166
Species (S)	1	1744	21.40	0.019
B*S Error (a)	2	245		
Water stress (W)	3	621	7.92	0.006
S*W	3	106	1.32	0.304
B*S*W Error (b)	12	470		
Time (T)	5	520	3.33	0.004
S*T	5	124	0.79	0.201
W*T	15	134	0.85	0.107
S*W*T	15	10	0.06	0.512
Error	80	156		
Corrected total	143	4954		

Table 8. Statistical analysis of osmotic potential on shattercane and woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	3.35	5.62	0.1511
Species (S)	1	8.30	13.93	0.0649
B*S Error (a)	2	0.59		
Water stress (W)	3	0.58	4.69	0.0514
B*W	6	1.20	9.61	0.0072
S*W	3	0.28	2.28	0.1799
B*S*W Error (b)	6	0.12		
Corrected total	23			

Table 9. Analysis of variance of CER of shattercane and woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	44.4		
Species (S)	1	84.1	5.27	0.040
B*S Error (a)	2	15.9		
Water stress (W)	3	184.8	4.46	0.007
S*W	3	18.7	0.45	0.923
B*S*W Error (b)	12	41.4		
Time (T)	5	66.4	3.16	0.033
S*T	5	23.5	1.11	0.231
W*T	15	28.1	1.33	0.196
S*W*T	15	20.8	0.98	0.251
Error	80	21.1		
Corrected total	143	4954		

Table 10. Analysis of variance of epicuticular wax content of shattercane and woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	4467	0.57	0.674
Species (S)	1	63809	24.28	0.016
B*S Error (a)	2	15608		
Water stress (W)	3	13221	23.04	0.022
S*W	3	9112	1.66	0.304
B*S*W Error (b)	12	5470		
Corrected total	23	112843		

Table 11. Analysis of variance of herbicide efficacy on shattercane

Source of variation	df	Mean square	F value	P > F
Block (B)	2	12.59	1.34	0.2706
Age (A)	1	2420.04	38.64	0.0249
B*A Error (a)	2	62.63	6.68	0.0028
Water stress (W)	3	3285.77	113.67	0.0001
A*W	3	88.59	3.06	0.0691
B*A*W Error (b)	12	28.90	3.08	0.0027
Herbicide (H)	3	1214.97	129.60	0.0001
A*H	3	24.84	2.65	0.0593
W*H	9	31.99	3.41	0.0026
A*W*H	9	10.06	1.07	0.39
Error	48	9.37		
Corrected total	95			

Table 12. Analysis of variance of herbicide efficacy on woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Block (B)	2	131.58	10.35	0.0013
Age (A)	1	5808.00	225.55	0.0044
B*A Error (a)	2	25.75	2.03	0.1643
Water stress (W)	3	1568.05	256.59	0.0001
A*W	3	170.50	27.90	0.0001
B*A*W Error (b)	12	6.11	0.48	0.89
Herbicide (H)	1	1302.08	102.46	0.0001
A*H	1	36.75	2.89	0.1084
W*H	3	55.13	4.34	0.0203
A*W*H	3	44.13	3.47	0.0410
Error	16	12.70		
Corrected Total	47			

Table 13. Analysis of variance of unabsorbed herbicide in shattercane

Source of variation	df	Mean square	F value	P > F
Blocks (B)	1	82.08	0.89	0.4148
Water stress (W)	3	62.63	0.68	0.6206
B*W Error (a)	3	92.11		
Herbicide (H)	1	4254.82	134.69	0.0014
B*H	1	764.50	24.21	0.0161
H*W	3	2.86	0.09	0.9603
B*H*W Error (b)	3	31.58		
Days (D)	3	1248.29	52.76	0.0001
B*D	3	117.19	4.95	0.0183
W*D	9	31.52	1.33	0.3149
H*D	3	122.47	5.18	0.0159
B*W*D	9	56.37	2.38	0.0812
W*H*D	9	20.03	0.85	0.5907
Error	12	23.65		
Corrected Total	63			

Table 14. Analysis of variance of unabsorbed herbicide in woolly cupgrass

Source of variation	df	Mean square	F value	P > F
Blocks (B)	1	6172.74	1389.42	0.0001
Water stress (W)	3	53.08	11.98	0.0354
B*W Error (a)	3	4.43		
Herbicide (H)	1	616.12	122.77	0.0016
B*H	1	632.37	126.33	0.0015
H*W	3	19.32	3.87	0.1481
B*H*W Error (b)	3	5.01		
Days (D)	3	479.55	14.73	0.0003
B*D	3	140.07	4.35	0.0281
W*D	9	16.46	0.51	0.8440
H*D	3	404.49	12.42	0.0005
Error	12	32.55		
Corrected Total	63			

Table 15. Analysis of variance of herbicide content in shattercane leaf cuticles

Source of variation	df	Mean square	F value	P > F
Block (B)	1	575.63	21.36	0.0191
Water stress (W)	3	125.29	4.68	0.1187
B*W Error (a)	3	26.94		
Herbicide (H)	1	2169.34	33.98	0.0101
B*H	1	146.35	2.29	0.2273
H*W	3	23.73	0.37	0.7810
B*H*W Error (b)	3	86.49		
Days (D)	3	359.18	15.36	0.0002
B*D	3	18.81	0.80	0.5158
W*D	9	43.63	1.86	0.1560
H*D	3	79.61	3.41	0.0533
Error	12	23.42		
Corrected Total	63			

Table 16. Analysis of variance of herbicide content in woolly cupgrass leaf cuticles

Source of variation	df	Mean square	F value	P > F
Block (B)	1	31.10	0.23	0.6667
Water stress (W)	3	4.20	0.03	0.9914
B*W Error (a)	3	137.20		
Herbicide (H)	1	1964.45	69.90	0.0036
B*H	1	44.98	1.60	0.2954
H*W	3	21.55	0.77	0.5841
B*H*W Error (b)	3	28.13		
Days(D)	3	158.51	2.38	0.1209
B*D	3	23.91	0.36	0.7842
W*D	9	19.37	0.29	0.9641
H*D	3	32.71	0.49	0.6952
Error	12	66.65		
Corrected Total	63			

Table 17. Analysis of variance of herbicide content inside shattercane leaves

Source of variation	df	Mean square	F value	P > F
Block (B)	1	31.95	6.22	0.0881
Water stress (W)	3	335.68	65.40	0.0031
B*W Error (a)	3	5.13		
Herbicide (H)	1	309.49	52.47	0.0054
B*H	1	0.01	0.01	0.9660
H*W	3	1.80	0.31	0.8218
B*H*W Error (b)	3	5.89		
Days (D)	3	156.69	8.41	0.0028
B*D	3	13.53	0.73	0.5554
W*D	9	18.63	1.00	0.4876
H*D	3	35.19	1.89	0.1852
Error	12	18.62		
Corrected Total	63			

Table 18. Analysis of variance of herbicide content inside woolly cupgrass leaves

Source of variation	df	Mean square	F value	P > F
Block (B)	1	67.50	13.64	0.0344
Water stress (W)	3	295.40	59.69	0.0036
B*W Error (a)	3	4.94		
Herbicide (H)	1	2.22	1.46	0.3133
B*H	1	113.28	74.43	0.0033
H*W	3	0.79	0.52	0.6965
B*H*W Error (b)	3	1.52		
Days (D)	3	39.88	5.76	0.0112
B*D	3	46.48	6.71	0.0066
W*D	9	4.04	0.58	0.7868
H*D	3	7.46	1.08	0.3956
Error	12	6.92		
Corrected Total	63			

Table 19. Analysis of variance of herbicide translocated to other shattercane tissues

Source of variation	df	Mean square	F value	P > F
Block (B)	1	50.09	14.32	0.0323
Water stress (W)	3	93.80	26.82	0.0114
B*W Error (a)	3	3.49		
Herbicide (H)	1	19.82	2.67	0.2006
B*H	1	20.49	2.76	0.1950
H*W	3	9.55	1.29	0.4199
B*H*W Error (b)	3	7.41		
Days (D)	3	87.69	33.94	0.0001
B*D	3	10.72	4.15	0.0311
W*D	9	10.52	4.08	0.0133
H*D	3	3.30	1.28	0.3263
Error	12	2.58		
Corrected Total	63			

Table 20. Analysis of variance of herbicide translocated to other woolly cupgrass tissues

Source of variation	df	Mean square	F value	P > F
Block (B)	1	216.49	43.20	0.0072
Water stress (W)	3	115.82	23.11	0.0142
B*W Error (a)	3	5.01		
Herbicide (H)	1	11.91	1.10	0.3704
B*H	1	40.18	3.73	0.1491
H*W	3	8.53	0.79	0.5737
B*H*W Error (b)	3	10.78		
Days (D)	3	21.07	2.49	0.1101
B*D	3	10.04	1.19	0.3560
W*D	9	2.17	0.26	0.9755
H*D	3	17.16	2.03	0.1637
Error	12	8.46		
Corrected Total	63			